UNITED STATES DEPARTMENT OF AGRICULTURE

FOREST SERVICE

Project No. (FS-INT-1603)

PHYSIOLOGICAL TOLERANCE LIMITS OF PLANT SPECIES SELECTED FOR REVEGETATION OF RANGE-WATERSHED HARSH SITES

Problem Analysis

by

Ray W. Brown
Research Forester

September 1966'

Intermountain Forest and Range Experiment Station
Forest Service
U. S. Department of Agriculture
Logan, Utah

PROBLEM ANALYSIS COVER SHEET

Research Unit:___Logan, Utah___WMR___ Project No.:_FS-INT-1603_____

Problem Analysis Title__PHYSIOLOGICAL TOLERANCE LIMITS OF PLANT_____

SPECIES SELECTED FOR REVEGETATION OF RANGE-WATERSHED HARSH SITES

_____

Author:__Ray W. Brown_____Date Prepared:September 1966_____

REVIEW RECORD:

Reviewer:	Function	Date
(signature)	_WMR 1704_	9/9/66
(signature)	" "	9/9/66
E.E. (signature)	_WMR 1603_	9/7/66

Approved by:

Unit Leader___Paul E. Packer_____ Date___9/9/66___

Concurrence
Division Chief__Asst. Director___O.L. Copeland___ Date__9-13-66__

DISTRIBUTION RECORD:

Office or Person	Location	Date
✓ O. L. Copeland	Ogden	
J. P. Blaisdell	Ogden	
Washington Office	Washington D. C.	
P. E. Packer	Logan	
R. W. Brown	Logan	
Files	Logan	

Project No. (FS-INT-1603)

PHYSIOLOGICAL TOLERANCE LIMITS OF PLANT SPECIES
SELECTED FOR REVEGETATION OF RANGE-WATERSHED
HARSH SITES

Problem Analysis

by

Ray W. Brown
Research Forester

September 1966

Intermountain Forest and Range Experiment Station
Forest Service
U. S. Department of Agriculture
Logan, Utah

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

INTRODUCTION

THE PROBLEM

Deteriorated range-watersheds resulting from exploitative use through overgrazing, together with bare exposed harsh sites maintained by severe montane and subalpine environments, have long been a matter of concern. Despite recent management innovations designed to improve these critical areas, extensive range-watershed deteriorated and harsh sites remain as primary sources of torrential floods and polluted stream-flow throughout the Intermountain Region. A number of attempts have been made by the Intermountain Forest and Range Experiment Station, dating back to the early part of this century, to develop management techniques through research to curb excessive soil erosion and establish a plant cover on these exposed areas.

A review of the accumulated results of these research efforts has revealed several interesting and conspicuous facts. First, the severe nature of environmental conditions, coupled with widely fluctuating microclimatic factors, provoke the persistence of these critically deteriorated harsh sites. Extensive research and field observations corroborate evidence that bare harsh sites exposed to extreme environmental conditions remain essentially bare indefinitely. Natural revegetation through migration of native plant migrules takes place very slowly, if at all, on these sites. The persistent caustic nature of the microclimate and overall environment of harsh sites has created conditions of plant cover depletion, and maintained a state of excessive habitat instability.

A second interesting fact offered by past research reveals that
the stabilization of harsh sites with a protective plant cover appears
impossible without artificial revegetation. Revegetation attempts
have purposefully been restricted to habitats known to support favorable
environmental conditions, while harsh sites have been avoided. In large
measure, the lack of revegetation success on poorer more exposed sites
is attributable to a lack of knowledge concerning plant-environment
relations. This ignorance is largely reflected by the fact that artifi-
cial revegetation attempts have followed rather empirical methods and
techniques. Although empirical, or trial-and-error, approaches have
provided much practical knowledge about revegetation, they have contri-
buted very little basic information that would be helpful in circumventing
severe environmental conditions relative to plant physiological-ecological
requirements.

The third, and perhaps most important, revealing fact is the lack
of basic knowledge concerning the physiological tolerance limits of
species selected for revegetation. It is perhaps significant that a
large part of the research in areas of resource management has largely
ignored the most obvious and primary agent through which management is
carried out: the plant! Little is really known about the physiological
requirements and tolerance limits of wild land plant species, particularly
relative to the effects of variations and fluctuations of severe environ-
mental factors. To adequately circumvent the rigorous environments of
harsh sites, and thus establish a protective plant cover on them, means
must be sought by which species can be provided an environment commensurate

with their physiological tolerance limits. However, before this can be
accomplished, detailed basic information concerning plant physiological
tolerances relative to environmental conditions must be acquired.
Although a considerable amount of physiological research has been done,
practically all of it has been directed toward crop plants of commercial
value. Many of the wildland native and introduced species that have
considerable importance to revegetation of harsh sites have been relatively
ignored from this standpoint.

OBJECTIVES

If harsh sites are to be eliminated as potential erosion and flood
source areas, they must be provided with a protective plant cover.
Drastic mechanical treatments of flood source areas, such as trenching,
have successfully been introduced as temporary preventive measures, but
as Bailey et al. (1947) advise, the only realistic approach to permanent
rehabilitation of critical sites is to eliminate the source of erosion
and overland water movement. The establishment of a protective plant
cover on severely exposed and deteriorated range-watersheds is the most
direct course to gaining habitat stability, a permanent check on unfavorable
environmental conditions, and restriction with eventual control of soil
erosion (Ellison 1949, Plummer et al. 1955). The most important and
basic approach to attaining these goals is through study of the funda-
mental physiological processes of plants, and their relations with the
factors of environment (Storey 1960).

This problem analysis is designed to provide a basis for the determination of the physiological tolerance limits of selected plant species in terms of environmental factors limiting to growth. These investigations will provide fundamental information in several vital areas. First, they will provide a basis for the determination of the degree of adaptation of each species to various conditions of environment. Second, they will provide a basis for the matching of species with specific harsh sites. Packer (1964) has explained the need for microenvironmental characterization studies on specific range-watershed harsh sites, and a separate problem analysis for this study is currently being prepared. Third, physiological studies will provide a basis for the determination of the methods and techniques of artificial revegetation. A separate problem analysis is also currently in preparation for the latter problem area. All three problem areas are closely interrelated, wherein their collective results will provide basic knowledge concerning a multitude of critical problems, as well as the fundamental issue of harsh site rehabilitation.

The analysis of the problem was begun by assembling pertinent literature concerning plant physiological processes and their tolerances and requirements relative to environmental conditions. A review of this literature outlines the status of current knowledge relative to physiological processes and tolerance limits, and forms the basis for further more detailed study of specific species to be selected for revegetation studies that have proved to be relatively well adapted to conditions of harsh sites. Priorities have been proposed for the various studies suggested, along with time schedules, facilities, and personnel needed.

ENVIRONMENTAL FACTORS AND PHYSIOLOGICAL RESPONSES

The potential behavior of the physiological processes of plants
is governed by the laws of evolution and genetics. The magnitude of
this behavior is a measure of plant physiological plasticity or variability
over the range of environments to which it is adapted. This range of
behavior is referred to as the physiological tolerance limits of the
plant. Physiological functions of plants are influenced and entirely
circumscribed by environment, but the limits to which these functions
may be performed are genetically controlled. A plurality of interrelated
environmental factors will trigger a physiological response or process,
but the latitude within which this process will function are stringently
controlled by the genetic code. When these limits are exceeded by the
environment, the plant can no longer perform vital physiological functions.
The universal impact of this principle upon all biological systems has
long been recognized, and has been widely expanded as a vital biological
tool (Bonner and Galston 1958, Leopold 1964, Morris 1960, Sampson 1959,
Billings 1957).

Through their influences on the physiological processes of plants,
the interrelated complex of individual environmental factors also control
plant distribution. Other impressive phenomena relative to the response
of plants to environmental influences, besides the establishment of limits
to range of habitation, are direct modification of the organism by an
environmental factor, and a regulation of sequential steps in the plant
life cycle (Leopold 1964). The range of persistence of environmental

responses are either short-term, slightly persistent, metastable, or repetitive rhythmic diurnal events.

The most important environmental factors affecting plant growth appear to be water, temperature, radiant energy, nutrition, and biological competition (Bonner and Galston 1952, Billings 1957). These five factors may be considered basic environmental ingredients, yet each is composed of many facets, and subject to many conditions. Environmental conditions of slope gradient and exposure are themselves not basic factors, but only serve to modify basic factors. Together with the complexity of the interrelations among individual factors, there is also an equally complex interlocking relation among environmental factors and the organisms they influence. Each species has its own cardinal point for each environmental factor, and throughout the life of the plant these requirements are in a constant state of flux. The physiological requirements of a recently emerged seedling are changing constantly with growth and maturity. Even within a growth and developmental stage, plant requirements vary with changing environmental conditions, such as mature plant metabolism interruption during flowering and fruit set. Also, the requirements for one factor which may be limiting in availability may be compensated for by a modifying environmental condition. Compensatory habitat conditions are common in nature, as for instance, soil texture compensating for soil moisture availability, soil color for surface temperature, and slope exposure for attendant radiant energy.

WATER

Water is the single most important component of the living plant. Water has four principal involvements with the living tissues of plants: (1) as the matrix for cytoplasm, water is an actual structural component of cellular substances; (2) as a reagent in biological reactions such as photosynthesis and in hydrolytic processes; (3) as a solvent in which salts and gases enter cells, and which facilitates their movement from cell to cell; and (4) is essential for the maintenance of the turgidity necessary for cell enlargement and growth (Leopold 1964, Kramer 1962, 1963, Kozlowski 1964). Leopold (1964) lists an additional function of water, wherein it constitutes a major form of temperature regulation.

On range-watershed harsh sites, there appear to be three principal concerns relative to the effects of water on plant physiological processes: (1) plant-water relations and physiological processes; (2) the effects of atmospheric moisture on growth and survival; and (3) the effects of atmospheric desiccation through wind action.

Plant-Water Relations and Physiological Processes

The single most important factor determining the success or failure of artificial revegetation is the availability of soil water (Hull and Holmgren 1964, Forsling and Dayton 1931, Cassady and Glendening 1940, Robertson and Pearse 1945, Levin and Springfield 1955, Plummer et al. 1955, Stoddart 1946, Stoddart and Smith 1955, Sampson 1959). The effectiveness of the soil in storing water for plant growth is affected by conditions of texture, depth and degree of development, landscape

physiographic features, and also by atmospheric conditions of humidity
and wind. Water availability is generally considered to be a more
limiting factor to growth at lower elevations, and temperature at upper
elevations (Humphrey 1962). However, interactions among environmental
factors create conditions whereby any one factor is never limiting all
of the time. At higher subalpine elevations windy conditions can be
of greater severity and create greater water deficits near the surface
despite whatever temperature gradients may exist between upper and
lower elevations. Also, soil water becomes progressively less available
with decreases in temperature (Ellison 1949, 1954, Bliss 1962).

Some habitats, because of attendant environmental interactions,
are more favorable sites in terms of water availability than others.
This is a particularly critical principle to artificial revegetation,
and has been the primary determining factor when choosing revegetation
sites. The availability of soil water is strongly influenced by soil
texture, wherein heavier soils are capable of retaining much higher
quantities than lighter soils (Buckman and Brady 1960). Ellison (1954)
found the soils of the subalpine communities on the Wasatch Plateau to
be rather heavy with a permanent wilting percent (PWP) averaging about
33 percent. On more heavily eroded exposed sites, the percent gravel
increased considerably. This has the general effect of greatly lowering
PWP. Also, north facing slopes are usually more mesic habitats than
south slopes, and east more mesic than west. This is greatly conditioned
by degree of slope, tending to be more xeric with steeper slopes.
Although seldom a matter of great concern at upper elevations, salinity

can greatly affect the availability of soil water (Gates et al. 1956).
Daubenmire (1957a) found that high elevation sites are particularly
well adapted to better conservation of available soil moisture. Summers
are short, and the active growing season is much shorter than at lower
elevations. The seasonal march of temperature raises the field capacity
(FC) in spring and lowers the PWP in the summer, and thus creates a
greater seasonal storage capacity.

Internal Water Balance

The essential feature in plant water relations is the internal
water balance, water stress, or degree of turgidity which exists in
plants because this is what controls those physiological processes
and conditions which in turn determine the quality and quantity of
growth (Kramer 1963, 1962, Kramer and Kozlowski 1960, Kozlowski 1964,
Leopold 1964, Slatyer 1957, 1960). Although a great deal of attention
has been paid to soil moisture stress and plant growth, plant water
stress is directly in control of growth, and only indirectly is it
controlled by soil water stress. It is the internal water balance within
the plant that controls physiological processes and not the availability
of soil water. Plant water stress depends on the relative rates of
water absorption and water loss rather than on soil water supply alone,
hence it is not safe to assume that a given degree of soil water stress
alone will be accompanied by an equivalent degree of plant water stress
(Kramer 1963). The essential features of internal water balance have
been discussed in many papers (Kozlowski 1964, Kramer and Kozlowski 1960,
Slatyer 1957, 1960, Kramer 1963, 1962) and will not be considered in any
great detail here.

Although soil water content cannot be used reliably as an index
to physiological processes and reactions to water deficits, its use as
a tool for indirect determinations of moisture stress effects is valuable.
For field use it has a wide range of applicability so long as it is
realized that what is being determined is soil water content and not
water stress within the plant. For many years the FC and PWP were
regarded as soil moisture constants which identified the upper and lower
limits of soil water available for plants. It is now agreed that water
is not equally available from the FC to PWP, but rather decreases sharply
as moisture approaches the PWP. However, unless the type of plant is
considered together with its stage of development and atmosphere condi-
tions, it is impossible to predict what level of soil moisture stress
will limit plant growth (Kramer 1963, Kozlowski 1964). Slatyer (1957,
1960) gives excellent accounts of the PWP as a constant for use in studies
of water stress effects.

The two principal processes regulating the internal water balance
in plants are absorption and transpiration. Water absorption is controlled
chiefly by soil factors and transpiration by atmospheric factors, hence
they often occur at somewhat different rates. The rate of water absorption
is controlled by rate of water loss, extent and efficiency of root
systems, environmental factors such as soil aeration, soil temperature,
concentration of the soil solution, and the free energy status of the
soil water (Kramer 1963, Kozlowski 1964, Slatyer 1957, 1960). The most
significant process of water absorption is passive, being entirely
controlled by osmotic forces. Although there is considerable disagreement

about terminology, it is generally agreed that the basic physical laws
of diffusion pressure and osmotic potential regulate the principal
absorption process (Slatyer 1957, 1960); however, metabolic absorption
through active processes may also be important (Kozlowski 1964).

Of the factors affecting absorption, low soil water potential appears
to be the most important (Slatyer 1960). It has a direct effect on
the water potential in the plant, since the soil water potential must
remain higher than the plant water potential in order to maintain an
absorption gradient. It is certain that the greatest resistance to
water movement occurs in the gaseous phase within the leaf-air interface,
and when the resistance in the roots reaches the transpiration resistance,
the plant dies of dehydration. Actual availability of water to plants
encompasses the ability of a plant to absorb water at the root surface,
capacity for movement of replacement water to the root surfaces, and
root growth into moist areas (Kozlowski 1964). The inability of some
species to produce root systems extensive enough for adequate water
absorption is an important factor in influencing plant composition and
survival. Most rapid water absorption occurs in approximately the root-
hair zone (Slatyer 1960, Kramer 1963, Kozlowski 1964), hence capacity
for root-hair formation is an important characteristic influencing water
economy of plants. Herbaceous plants develop more root hairs than
woody plants, and angiosperms more than gymnosperms (Kozlowski 1964).

The primary factor causing water movement through the leaf is
transpiration. Practically all the water taken up by the plant ultimately
is lost to the atmosphere by this process. The overwhelming bulk of

transpiration occurs through leaf stomates (Kozlowski 1964, Pallas et al. 1963, Zelitch 1963). Transpiration is purely a passive process, the rate of which is determined by the vapor pressure gradient between the leaf and the outside air and by the various resistances to water movement in the transpiration path (Slatyer 1960). The main source of water resistance appears to be in the air layer adjacent to the leaf surface, in which a steep diffusion gradient is found leading to the freely circulating air beyond the leaf surface. The four principal factors affecting transpiration rate are: (1) water deficits, (2) light intensity, (3) temperature, and (4) CO_2 content within the stomatal structure.

In general, stomatal closure begins with an internal water balance deficit (Zelitch 1963, Slatyer 1960). With as little as a 10 percent decrease in total cell turgidity, stomates begin to close. Throughout the summer months, as the soil continues to dry, the stomates close earlier each day until the total soil moisture stress reaches a point whereby they stay closed, transpiration ceases, and photosynthesis falls off, causing death (Kozlowski 1964, Pallas et al. 1963). Mooney et al. (1965) found that plants on wet sites transpire more than plants on dry sites. On hot days transpiration may well exceed absorption, whereby the soil moisture stress becomes so great as to create higher resistances to water absorption than those controlling transpiration. Usually at night this imbalance is corrected, but if soil moisture is depleted enough in the regions surrounding the root, the plant will die.

Thus, the major factor controlling transpiration rate appears to be the internal water balance within the plant. However, with light

intensity increases, as in the morning, stomatal opening will occur
as a result of the effect of light on CO_2 concentration. As the CO_2
decreases, as a result of photosynthesis, the stomates will open.
However, if a midday water deficit occurs, stomates will be forced
closed by a collapse of the guard cells. Normally, rising temperatures
have the effect of causing stomatal opening, but if the temperature causes
a great increase in respiration with an accompanying increase in CO_2
concentration, the stomates will close as the result of increased water
deficit.

Effects of Water Deficits

Water is important to revegetation primarily as it affects the
survival and development of the plant from germination, through vegetative
growth and reproduction. Since moisture stress affects processes of
water absorption, root pressure, seed germination, transpiration,
photosynthesis, respiration, enzymatic activity, growth of shoots, roots,
reproductive organs, nutritional uptake, physiological temperature range,
and other factors, water is then clearly the most important factor
affecting revegetation success under most circumstances.

Although it is rare under natural conditions that germination
of viable seed becomes a real problem limiting revegetation success,
on harsh sites wide fluctuations in available soil water may require
special consideration of this growth stage. Under conditions of extended
drought, seeds frequently will not germinate if moisture is not available
to initiate growth. Kozlowski (1964) cites evidence indicating that
increased metabolic activity in seeds must necessarily precede germination,

and is a function of protoplasmic hydration. Knipe and Herbel (1960)
show that, for a seed to obtain moisture from the soil, it must overcome
two main forces: (1) the surface action of soil particles which account
for the matrix tension of soil moisture, and (2) osmotic tension due to
dissolved materials in the soil solution. Amen (1963) indicates that
in many cases of seed dormancy, water is an important factor in removing
growth inhibitors. Hunter and Erickson (1942) found that the require-
ments for water at germination may be much different than that for
growth of the plant. The maximum moisture tension under which germination
will occur is highly variable. Knipe and Herbel (1960) used mannitol
solutions to show that increasing osmotic concentrations to 20 atmospheres
prevented germination. McGinnies (1960) found with grass species that
at lower than optimum temperatures, at any moisture level, germination
is greatly retarded. Maynard and Gates (1963) found that germination
of crested wheatgrass will occur under a wide variety of moisture condi-
tions, but following germination moisture is required above the physiological
drought susceptibility level. Younis et al. (1963) found similar results
with alfalfa varieties.

It is clear that water deficits in meristematic regions reduce
growth materially (Kozlowski 1964). The most critical period of growth
in the establishment of vegetation is the seedling stage. If a seed
germinates later in the season than the time of optimum moisture condi-
tions, the receding zone of moisture in the soil may exceed the growth
rate of young roots. However, Kozlowski (1964) indicates that younger
tissue may be more drought resistant than older tissue. Ursic (1961a)

found that drought is the leading cause of first-year mortality on all
sites of loblolly pine seedlings. Frischknecht (1951) found that fall-
seeded species of range grasses are stimulated to faster growth at times
of optimum soil moisture than spring-seeded plants of the same species.
Seedling sensitivity to drought has been widely observed (Nord 1965,
Potter 1953), but Kozlowski (1964) shows that young tissues recover
more rapidly from drought than older tissues.

Water deficits are known to reduce photosynthesis because of an
increased resistance of CO_2 diffusion caused by stomatal closure and
also because of decreased permeability of mesophyll cells (Kozlowski
1964). This brings up the point of water-use-efficiency, whereby the
more efficient water users are better able to survive under periods
of moisture stress. Efficient water users are not more drought resistant,
but are better able to produce more photosynthate per-unit of water
used. Cheatgrass is a case in point, whereby Hull (1963) showed that
this species requires only 66 percent of the water needed by native
perennial grasses for each unit of dry matter produced. Woody species
are less efficient water users than perennial and annual herbaceous
vegetation (Humphrey 1962).

Relative to drought resistance, plants may be classified as either
drought escaping, drought evading, or drought enduring (Iljin 1957,
Kozlowski 1964). Drought escaping plants would be the least desirable
for harsh site revegetation since these include annual plants with
brief growing cycles. Iljin (1957) defines drought resistant species
as those which develop normally in "dry" habitats and yield maximum

crops. Obviously, drought resistance is a qualitative classification,
where each species has particular qualities relative to some reference
environment. However, the importance of drought resistance has been
widely discussed relative to revegetation (Humphrey 1962, Oosting 1959,
Kenesarina 1959, Craddock and Forsling 1938). Bailey (1940) found that
the best indication of the drought resistance of a species is a small
loss of total physiological water prior to permanent wilting. Julander
(1945) shows evidence which indicates that heat tolerance is an indication
of drought resistance. Daubenmire (1943) found that soil moisture availa-
bility is the prime factor controlling the lower distribution of vege-
tation in the Rocky Mountains. The role of drought resistance in the
distribution of vegetation has been thoroughly discussed by Klikoff
(1965b), Ruf (1966), Ellison (1949, 1954), and Daubenmire (1959).

The time of year when moisture is deficient is always a critical
factor, and is an important consideration in the introduction of species
for revegetation. Maximum growth is usually made when moisture is most
abundant (Daubenmire 1959, Kozlowski 1964). Warm-season species intro-
duced into a cool-season habitat could not survive because of summer
drought. Nelson (1934) found that time of precipitation relative to
the initiation of growth of black grama is vital, since precipitation
during the previous season completely controls growth rates during the
current season. Cathey (1964) indicates that growth retardants can
be used to suppress growth during unfavorable periods, while through
leaching, can be naturally eliminated during periods of optimum growth
conditions. The selective time of use of growth retardants would be

most useful for retarding seed germination during the fall, and aiding plants to resist wilt during unfavorable climatic periods. Singh and Alderfer (1966) found that the greatest damage to crops from moisture deficits occurs when the greatest soil water stress coincides with periods of the greatest atmospheric stress.

Kozlowski (1964) emphasizes the importance of continuous water availability for flowering. Daubenmire (1959) also emphasizes its necessity during fruit set. Optimum moisture conditions will usually promote maximum flower production (Nelson 1934, Lang 1952).

Atmospheric Moisture Effects

Although practically all of the water absorbed by plants is taken in through the roots, at certain times and under certain conditions absorption of water as dew or humidity may play an important role in the water economy of plants. In general, it appears that most of the water absorbed by leaves is through the cuticle (Slatyer 1960). Rate of absorption is markedly affected by the potential gradient from air to leaf, wherein the initial rates of uptake are greatest, and decrease progressively as the leaves regain turgor and the gradient is reduced.

According to Daubenmire (1959), perhaps the most important aspect of atmospheric moisture is its effect on transpiration rate. With all other factors remaining constant, it would be expected that an increase in relative humidity will result in a decrease of water loss from the plant because the vapor pressure gradient between the air-leaf surface would be decreased. Fog may augment the soil water in the immediate surface of desiccated soil, either by direct contact, or by condensing

on foliage surfaces and dropping to the soil. Many mosses and lichens extract moisture directly from the air.

There are a few reports that dew absorption by plants may subsequently be released into the soil through the root system (Billings 1957, Slatyer 1960, Kozlowski 1964). Kozlowski (1964) cites evidence that shows that ponderosa pine in soil near PWP was able to survive because of a resaturation of the needles, with a consequent reduction in the amount of water removed from the soil. This may have the effect of sustaining a severely stressed plant until water is again made available. Slatyer (1960) feels that the main importance of humidity or dew is its direct effect on lowering transpiration. Because of the small amounts of water absorbed by leaves, and because the rate of transfer also appears to be fairly slow, the amount of water transferred is probably usually not significant to affect the turgor in other parts of the plant. He attributes this slow rate of transfer to the extreme resistance of the leaf cuticle to water entry. Also, in most cases in nature, a favorable moisture vapor pressure gradient occurs very rarely. Also, the amount of dew available, or humidity, is in considerably lower quantities than water requirements of the plant. In the case of dew, it usually occurs at times when transpiration is negligible, yet remains on the leaf after sunrise thus reducing transpiration and permitting photosynthesis at the same time.

If atmospheric moisture is to be of any real benefit to the plant, it must reestablish a positive turgor pressure in the active tissue. There appears to be considerable disagreement on this subject, but

there can be little doubt that it can be beneficial, and definitely warrant further research (Billings 1957, Slatyer 1960).

Atmospheric Drought Effects

The principal agent of atmospheric drought, especially as it applies to exposed environments, is wind. Wind is primarily a modifying condition of environmental factors, affecting soil water content in the surface layers and air temperature. However, wind may have severe effects on the rate of transpiration, structural form of plants, soil surface stability, and the transport of plant migrules. Wind has been reported to have a significant influence on plant surface temperatures, but its most important physiological effect relative to harsh sites is on water desiccation of plant tissue (Kozlowski 1964, Oosting 1956, Daubenmire 1959, Bliss 1962).

In still air, transpiration tends to maintain a satisfactory balance with water absorption, but with strong air movement the layers of humid air which have accumulated adjacent to the plant surfaces are removed. With this action, wind drastically increases the rate of transpiration. The consequences of this action have vital physiological implications in cold habitats where moisture availability and protoplasm permeability are low (Daubenmire 1959). In the northern Rockies and Wasatch Mountains of Utah, chinook winds appear suddenly, raising the evaporative power of the air before the soil has warmed, and the ability of plants to maintain a satisfactory water balance is thus severely reduced. Ellison (1954) found the average wind speed at 18 inches above the ground surface in an herbaceous vegetation type of the Wasatch Plateau to be

3.76 m.p.h., with little seasonal variation. Marston (1956) found
that the average wind velocity over an open stand of herbaceous vege-
tation at 8,200 feet in elevation to be 3.29 m.p.h. during the growing
season, and 0.72 m.p.h. under a stand of aspen. Klikoff (1965a) found
wind velocities at between 10,000 and 12,000 feet in the Sierra Nevada
to average about 7 to 10 m.p.h. between the hours of 09:00 and 18:00.
However, gusts of from 30 to 40 m.p.h. are common. Wind at night is
usually negligible.

Carroll (1943) found that a 3 to 4 m.p.h. wind when the temperature
is 35°C and the relative humidity is 20 percent is lethal to all but
pre-hardened species. Even if soil water content is high, a dry wind
may accelerate transpiration rate to the extent that the resistance
of water to root absorption may be sufficient to create a serious
imbalance between transpiration and absorption. In this case, absorp-
tion cannot keep up with transpiration. Larson (1965) found that wind
causes a pronounced downward shift of growth increment toward the stem
base in tamarack. Wind also greatly reduced height growth. Satoo
(1962) found with black locust that wind at 7 to 8 m.p.h. depressed
growth and development significantly more in drier soils. Wind at
low velocities may actually increase growth by increasing the supply
of CO_2, but its main effect is one of transpiration acceleration. Also,
the harmful effects of wind are compounded by duration, being most severe
on the windward side of plants. Satoo also found that transpiration
increases suddenly with increased wind velocity, but levels off after
wind continues to increase.

Wind also dries a moist soil surface very rapidly by evaporation.
Soil loses water by evaporation more rapidly than a free water surface
because of the large amount of total evaporative surface presented
by the minute irregularities (Daubenmire 1959). Surface evaporation
can desiccate a soil to a depth of 2 to 3 dm., with severe consequences
to the survival of young seedlings. Definite quantitative data concerning
the physiological-ecological effects of wind are lacking, and its
importance clearly warrants further detailed consideration.

TEMPERATURE

Plant physiological activities are essentially restricted to a
temperature range of from $0^\circ C$ to about $50^\circ C$. At lower temperatures
physiological activities are limited by the freezing of water, and
at upper temperatures by heat denaturation of proteins. Temperatures
affecting plants are dominated by the diurnal flow of radiant energy
from the sun. The primary effect of temperature on plant growth is
one of controlling the rates of biochemical reactions, and altering
the physical changes in tissues which control the equilibria of enzyme
reactions, and quantitatively controlling what reactions will occur
(Leopold 1964).

Of all the environmental factors of importance to artificial
revegetation, temperature and the availability of soil water have
probably received the most attention. When soil moisture is readily
available, temperature will usually be the most limiting factor to
plant survival. For this reason, and because of its ease of study,

temperature conditions in the natural plant microenvironment and its
effects on the physiological-ecological processes of plants have been
widely studied. Also, its importance to physical factors of the environ-
ment have been extensively investigated. For instance, the availability
of soil water is greatly influenced by temperature. Absorption of
water is impeded by low temperatures by the direct process of decreasing
membrane permeability, and indirectly by increasing fluid viscosity and
surface tension (Kozlowski 1964, Slatyer 1960). Daubenmire (1957a)
found that rising summer temperatures in cold habitats decrease the
wilting coefficient sufficiently to increase soil moisture availability
equivalent to an addition of 12 mm. of precipitation. Anderson (1947)
found that soil freezes to a depth of 36 inches or more on bare sites,
and that freezing and heaving occur 17 days earlier and 45 days later
on bare sites than on grass-covered sites. Hermann (1963) considers
latitude, exposure, steepness of slope, vegetation cover, and soil
physical properties as the most important factors determining the
temperatures of soils. Scott and Burgy (1956) found infiltration rates
increase significantly after treatments up to temperatures of $300^{\circ}C$
in the 0 to 1/4 inch soil zone. Baum (1949) found that the temperature
gradient from 0.5 feet above the ground surface to 5 feet above is
very steep, often representing a difference corresponding to an elevation
relief difference of 600 feet. Decker and Ronninger (1957) found that
frost heaving in soils decreases with depth and increasing plant cover.

Temperature influences practically the entire spectrum of physio-
logical processes, including photosynthesis, respiration, cell division

and elongation, enzymatic activity, chlorophyll synthesis, and trans-
piration. A generalized temperature-response curve for the growth of
plants closely follows the shape of an enzyme-response curve, rising
rapidly in the lower temperature ranges of 0 to $15^{\circ}C$ and less rapidly
in the intermediate range of 15 to $30^{\circ}C$, and then falling rapidly at
high temperatures (Leopold 1964, Kramer and Kozlowski 1960). Like
enzyme activities, growth rates are more than doubled by a $10^{\circ}C$ rise
in temperature. It is apparent that temperatures are important to the
survival and growth of plants in harsh sites, particularly as these
processes are affected by high and low temperatures, as well as the
diurnal phenomenon of thermoperiodism.

High Temperature Effects

The principal effects of high temperatures on plant growth are
tissue desiccation, imbalancing photosynthesis and respiration, and
injury to protoplasm. With other factors remaining constant, an increase
in air temperature activates the rate of water use, hence the rate of
transpiration is increased. This has the principle effect of rapidly
depleting the available supply of soil water. The optimum range for
photosynthesis is usually somewhat lower than that for respiration.
As temperatures increase, the rate of photosynthesis decreases, and
that of respiration increases beyond the normal physiological balance
of the plant. The thermal death point usually lies but a few degrees
above the optimum temperature for growth, but growth may be restored
by addition of a single substance (Langridge 1963). If temperature
continues to rise, more substances are progressively required, such as

additional nutrients, shade, water, and others, until the requirement becomes so large that the environment can no longer supply them, and death results. With rising temperatures the plant enters a quiescent state, sometimes accompanied by chlorosis, then dies with the further inactivation of enzymes (Daubenmire 1959).

High temperatures are normally detrimental to dormant seeds, principally because the higher temperatures increase the rate of food reserve respiration. Laude et al. (1952) found that with soil surface temperatures of $127^{o}F$, six species of grass being studied would not germinate. The closer the time of emergence of seedlings to the high temperature treatment, the lower the germination rate.

Excessive temperatures are most liable to occur in the field as a consequence of intense illumination. Plants are subjected to a heat load or thermal stress by radiation. When subjected to this heat load, plants redistribute the absorbed heat in the form of reradiation, convection and conduction, and transpiration or evaporation (Gates and Benedict 1963). By these mechanisms, the temperature of the plant remains below the lethal threshold unless the heat load becomes unusually heavy. Leaves in strong sunlight may reach temperatures of 10 to $15^{o}C$ higher than the surrounding air, and bulky tissues may reach $30^{o}C$ higher (Leopold 1964). As a cooling agent, transpiration clearly contributes to the heat balance of the plant by helping to dispose of about one-third of the heat energy received. Zelitch (1963) describes the transpiration process, and the effect of temperature on stomatal behavior. The essential influence of temperature on stomates is to cause them to open, which allows for more rapid tissue cooling.

The temperatures at which injurious reactions set in vary markedly from plant to plant. Early stages of seedling development warrant particular study relative to heat tolerance. Laude and Changula (1953) found with bromegrass that for the first 3 to 4 days following emergence, young seedlings are tolerant of temperatures up to 130°F at a relative humidity of 30 to 35 percent for a duration of 4 3/4 hours. However, maximum heat injury occurs between the ages of 7 and 28 days. Apparently, unused food reserves in the seed endosperm are responsible for the increased tolerance of young seedlings. Lethal seedling temperatures vary with the duration and intensity of the temperature. Soil surface temperatures of 130 to 160°F are commonly recorded on bare sites, but the effects of shading commonly reduce temperatures by 20 to 35°F (Koshi and Stephenson 1962, Maguire 1955, Hellmers 1963).

The roots of plants in undisturbed soil are generally deep enough to escape injury from excessive heat. Deeply cultivated soil with a highly irregular surface exposes a greater surface area to heating, and increases the chances of heat injury. Ursic (1961b) found that the roots of young loblolly pine seedlings are tolerant of temperatures to 46°C for two hours without appreciable mortality.

In connection with the protein-denaturation involvement in high temperature damage, Leopold (1964) indicates that much damage can be prevented with the application of kinetin. This chemically imposed heat resistance is attributed to kinetin stimulation of protein synthesis. Langridge (1963) presents an excellent broad review of the biochemical effects of extreme high temperatures on plant growth. Relative to

tree physiology, Kramer and Kozlowski (1960) indicate that the thermal
death point of living cells seems to be about 50 to 60°C, but is highly
variable.

It has been fairly well established that growth rates and other
physiological processes increase with rising temperatures. However,
the interaction of other environmental factors frequently modifies
this generality; wherein, for instance, a water deficit associated
with high temperatures may result in a slowing down of growth with
eventual death. Jones et al. (1963) found that temperature greatly
influences growth rate as modified by fertilizer. When temperatures
reach 55°F, soft chess growth rate is not altered by ammonia fertilizer,
but at higher elevations at lower temperatures growth was increased.
Weihing (1963) found that temperature has a greater influence on rye-
grass growth than solar radiation.

The resistance of living plant tissue to heat is thought to be
indicative of its survival under extreme conditions of drought, hot
temperatures, and fire (Jameson 1961). Lethal temperatures in all
plants are highest in the winter and lowest in late spring, with woody
plants having a higher resistance than herbaceous plants. Jameson
(1961) estimated that near-lethal temperatures to grass plants are
reached every summer on the soil surface. Julander (1945) found that
species originating in warm, drier habitats are more tolerant of high
temperatures, and concludes that heat tolerance is related to drought
resistance. Plants from xeric habitats tend to resemble hardened plants,
in that their food reserves of sucrose and total carbohydrates are

high. A high heat load exerted on the plant triggers a cooling reaction through transpiration. If moisture conditions are unfavorable, transpiration may tend to deplete, and eventually exhaust the water supply. Tew et al. (1963) found that increasing soil temperatures increase the rate of plant transpiration. Thames (1961) studied various wax coating substances on the surface of the leaves of Pinus taeda and their effect on transpiration rates. He concluded that wax, as a transpiration retardant, grossly reduced survival because the surface temperatures of treated leaves increased 4.4°F. Wax acts as a temperature trap, and as such, causes a large increase in the vapor pressure gradient between the leaf and atmosphere.

Damage to plants by high temperatures involves the imposition of stresses on the cytoplasm (Leopold 1964). High temperature hardiness involves a retardation of evaporative loss rates. An additional effect of high temperature is the denaturative action on the plant proteins. The formation of toxic substances may be a consequence of protein-denaturation activities, and the hardening reaction may involve an increase in protein synthesis. It has been suggested that the development of hardiness may be a result of increases in the viscosity of the cytoplasm and a resulting higher degree of water binding in the cells.

Air temperature in an environment is an influential factor in determining plant distribution. Klikoff (1965a & b) found that photosynthesis rates of native species under temperature stress parallels their distribution. Xeric species achieve their maximum rate of photosynthesis under relatively warmer and drier conditions than more mesic

species. Through genetic variation, some groups of plants have success-
fully adapted themselves to local temperature fluctuations. Daubenmire
(1957b) found coastal ecotypes of species not generally adapted to
endure climatic variations as well as inland ecotypes. Rogler (1943)
found that at -10°C northern strains of warm season species showed
higher survival rates. Cool season species with a southern origin are
less resistant to subzero temperatures than those of northern origin,
but cool season species are more resistant than warm season species.

Low Temperature Effects

There are three main phenomena involved in plant injury and killing
by low temperatures: (1) proteins may be precipitated directly above
the freezing point of water; (2) intercellular ice may form, drawing
water out of the protoplasts, resulting in dehydration and an irrever-
sible precipitation of protoplasm, and (3) ice forming in the protoplast
is nearly always fatal because crystal growth disrupts protoplasmic
organization (Daubenmire 1959).

Frost damage can occur at air temperatures scarcely in the freezing
range because leaves have a ready ability to radiate heat to the sky
and so are cooled below the air temperature, especially at night
(Leopold 1964). There is some effect of ice crystals rupturing cell
walls after freezing, but the main effect of low temperatures is the
physical disruption of the cell contents by the movement of water out
of the cells. Rapid freezing is much more damaging than slow freezing,
because with the former, ice crystals form in a haphazard manner through
the tissues, while in the latter case, there is a preferential formation
of crystals between the cells.

A plant is not equally resistant to low temperatures at all stages of its life cycle. Seeds are generally the most resistant among the various stages of growth. In some species, a cold pretreatment through stratification is needed to destroy the lipids in the seed to break dormancy (Aman 1963). Hull (1960) found that germination of intermediate wheatgrass was accomplished at temperatures slightly above freezing under 70 to 77 inches of snow. Gritton and Atkins (1963) found that subfreezing temperatures for a duration of four hours cause severe reductions in seed viability of sorghum when moisture content is greater than 25 percent. Ashby and Hellmers (1955) found a wide variation in low temperature resistance among the seeds of 20 species of grasses and alfalfa.

The ability of a parasitic fungus to gain entrance into, as well as to develop within, a host organism is often strongly conditioned by temperature. Laude (1956) found that decreasing temperatures often increase pathogen injury to seed. A pre-chilling treatment of seeds of six grass species at $20^{\circ}F$ at an 18 to 20 hour duration reduced germination 90 percent due to pathogen injury. Bleak (1959) found that early-fall germinated seed of grasses are killed in spring due to low temperatures. Desiccation due to freezing renders seed susceptible to pathogenic injury under snow in winter conditions. Bleak (1963) found, however, that low temperature pretreatments are necessary for germination of many species at high elevations. Bleak (1963) has made extensive studies of the effect of Podosporiella verticillata on the germination and growth of many grass species in the Intermountain Region.

Of the various environmental factors, temperature is the most important limiting factor with regard to plant growth and development in cold habitats (Bliss 1962). Each physiological function is performed at a maximum rate at an optimum temperature, but the optimum may not be identical for all functions. Rosenquist and Gates (1961) studied various range grass species in terms of physiological processes and the effects of temperatures on them. Their results indicate that as temperatures exceed or retreat from the optimum, physiological efficiency decreases. Smith et al. (1965) found that periods of warm weather in the spring, followed by a period of unusually cold temperatures cause severe damage to recently emerged seedlings of bitterbrush. Arakeri and Schmid (1949) found that grass seedlings are better adapted to survival under temperature stresses of $-10^{\circ}C$ for eight hours than legumes. Miller and Bunger (1963) found that by spreading a clear plastic film over rows of planted corn, the resulting increased soil temperatures encourage the emergence and development of seedlings earlier in the season. This could be useful in the early spring when air temperatures are warm but soil temperatures remain cold. This practice would encourage earlier germination and allow young seedlings to take advantage of a longer period of favorable moisture. Decker and Ronningen (1957) found that frost heaving tends to decrease with an increase in plant cover.

There are various beneficial effects to be derived from cold temperatures. The promotive effects induced by low temperatures is called vernalization. Vernalization is usually reserved for discussions of flowering, wherein with the seasonal march of temperature through

the summer and into fall temperature begins to decline. This signifies
an ecological coordination of flowering times in most temperate grasses
and other plants. On the other hand, a temporary low temperature effect
promoting seed germination is usually called stratification, but it too, is
really vernalization (Leopold 1964). Temporary protoplasmic adaptation
affecting a measure of immunity to low temperature injury is called
hardening. Frischknecht (1951) considers the ability of a species to
harden increases its survival chances; however, the ability to respond
to favorable environmental conditions through growth is more desirable.
In harsh climates an accumulation of anthocyanin pigmentation indicates
a buildup of carbohydrate reserves in the leaf tissues, hence hardening
to cold temperatures. Hardening does not prevent the formation of ice
crystals, it merely alleviates their damage. Thus, hardening is merely
inducing resistance through exposure to low temperatures (Leopold 1964).
Kenefick (1964) defines cold acclimation as the primary biological adjust-
ment to cold temperatures as determined over a period of time at a certain
temperature. Acclimated plants wilt and slow down their physiological
processes when temperatures drop, and thus escape the lethal effects of
freezing. Cathey (1964) indicates that various growth retarding chemicals
induce frost hardiness.

There are several stimulating effects of low temperatures on growth
and reproduction which warrant further study. Aside from the low-
temperature effects on seed germination, the chilling requirements of
dormant buds of many shrub and tree species require consideration. Many
shrubs, such as sumach, rose, elderberry, and blueberry require winter

stimulation with temperatures ranging between 5 and 8°C for various periods of time, depending upon the species, before dormancy in the buds will be broken to permit renewed spring growth. If these species are introduced into climates with temperatures that persist for longer periods than adaptation permits, a response to winter stimulation will result in severe winter-kill of young growth primordia. In some species, especially those from high elevations, a thermoconductive pre-treatment or vernalization is necessary for flower production.

Thermoperiodism

The relation between day and night temperatures has marked effects on the growth of various herbaceous species; this phenomenon is termed thermoperiodism (Kramer 1957, Leopold 1964). The beneficial effects of a differential day and night temperature seem to be characteristic of whole plants. A lowered night temperature leads to large improvements in the quality of growth, and the earliness and intensity of flowering. There is considerable disagreement among physiologists about the exact mechanism involved in the beneficial effects of differential temperatures, but there is little doubt that they improve growth. Kramer (1957) found that for loblolly pine seedlings, the amount of shoot growth triples when day temperatures are increased from $17°C$ to $30°C$, and night temperature maintained at $17°C$. The closer the day temperature approximates the night temperature, the less growth is made. Best growth is made with the widest spread. Longer photoperiods increase the growing season length, but do not change the basic growth pattern due to thermoperiodism. Peterson and Loomis (1949) found that with

increased temperatures and photoperiod, the greatest yields in Kentucky
bluegrass are obtainable. Some species require a critical photoperiod
combined with critical temperature ranges to induce flowering. This
is particularly true of short-day plants such as orchard grass which
will flower only after the long days and warm temperatures of summer
shorten and cool to slightly above freezing (Gardner and Loomis 1953).
Temperature may act as a compensatory mechanism for daylight, wherein
cool temperatures may offset the requirements for long days to induce
flowering (Britten 1961).

RADIANT ENERGY

Perhaps of all the environmental factors affecting the physiology
of plants relative to artificial revegetation, radiation has been the
least studied. It is the process by which energy is propagated through
free space by virtue of joint undulatory variations in the electric
and magnetic fields in space (Reifsnyder and Lull 1965). This transfer
of energy occurs at the speed of light, does not depend on the presence
of matter, and as a process exhibits both wavelike and particulate
phenomena. Wavelengths important in transferring energy to the earth
from the sun range from about .1 micrometer (μm) to 4 μm, and is referred
to as short-wave radiation. About 10 percent of this energy is in the
ultraviolet region of the electromagnetic spectrum from .1 to .4 μm;
the remainder is about equally split between visible light between .4
and .7 μm, and infrared radiation from .7 μm to 4 μm. Radiation is
emitted from the earth's surface and the objects on it in the long-wave
infrared region from 4 μm to about 100 μm.

Radiation is a form of energy that can be transformed into work, heat, or potential energy of food in the plant (first law of thermodynamics). The spontaneous transformation of concentrated light energy into potential energy, such as protoplasm, is never 100 percent efficient because of its dispersion into cooler surroundings as heat (second law of thermodynamics). Thus, radiant energy is responsible for biological production through photosynthesis, reproduction, and the chemosynthesis of complex biochemical substances (Leopold 1964). As such, radiation directly or indirectly affects factors of the energy budget and flow in physiological systems (Gates 1962).

Radiant energy streams to and from the surface of the ground and all objects on it. The magnitude of these streams of energy, their direction, spectral composition, and distribution through time control the energy available for heating surfaces, evaporating water, supporting photosynthesis, and in general, for making life possible (Reifsnyder and Lull 1965). The total sum of this energy constitutes the radiation balance or radiation budget. The radiation budget is composed of the following energy fluxes: direct short-wave radiation directly from the sun, diffuse short-wave radiation from the atmosphere, reflected short-wave radiation from the earth's surface, downward long-wave radiation from the atmosphere, and upward long-wave radiation from the earth's surface (Gates 1962, Reifsnyder and Lull 1965).

Physiologically and ecologically, the quality of radiation (wave length), the intensity (gram-calories per unit of time), and duration (length of day) are known to be important.

Radiation Quality

The quality of solar radiation reaching the earth's surface varies
with latitude, altitude, season, time of day, and local obstructions
in the atmosphere and by vegetation. Moisture in the atmosphere tends
to absorb light in the blue and red regions of the spectrum, allowing
less effective light for growth in the green spectral region to penetrate
(Bonner and Galston 1958). Under a forest canopy, the shaded understory
vegetation receives a depressed incidence of blue and red, but a high
incidence of green and other light in the central regions of the spectrum,
and high quantities of infrared light (Bonner and Galston 1958, Oosting
1956).

Although light quality is seldom a principal limiting factor in
the natural environment (Daubenmire 1959), some important considerations
relative to red/far-red light ratios and other quality effects should
be made. The importance of light quality lies in its effect on phyto-
synthetic and chemosynthetic processes. In general, there appear to
be three major types of action spectra for plant responses: (1) those
driven maximally by both red and blue light (photosynthesis, some
tropisms, and plant movements); (2) those driven maximally by red light
(chorophyll formation, photoperiodism, seedling morphogenetic responses,
and dormancy responses); and (3) those driven maximally by blue light
(phototropism, and polarization responses) (Leopold 1964). Because of
its importance to seed germination and seedling growth, the red/far-red
ratio probably exerts a dominant influence in the natural environment.

In plant physiological systems, the effect of red light is reversible by far-red light, and is due to the absorption characteristics of a pigment called phytochrome (Siegelman and Butler 1965). Amen (1963) indicates that this reversible photoreaction mechanism is present in all seeds, but is not always obligatory for germination. Germination appears to be enhanced by exposure to red radiation and diurnal alteration of temperature, but this promotive effect can be negated by far-red radiation. Light sensitive seeds respond differently to light at different temperatures, the light requiring response increasing with increased and decreased temperature. However, the germination of most seeds under natural conditions takes place in darkness, wherein the mesocotyl (in grasses) begins penetration through the soil. The termination of mesocotyl growth, and the commencement of leaf growth, is triggered by red light (Leopold 1964). At higher light intensities, shorter wave lengths may also be effective in this procedure. The higher incidence of ultraviolet at high elevations has been attributed as a partial cause for the dwarf-like structure of alpine plants, but Bliss (1962) discounts this theory. In some plants, particularly short-day plants, a red light stimulus is inhibitory to flower induction (Lang 1952). With increasing far-red light exposure, the inhibitory effect is removed. Cumming et al. (1965) studied the action of phytochrome relative to flowering in Chenopodium rubrum.

Radiation Intensity

The gram-calorie unit of energy sums the radiation of invisible and visible wavelengths. Light alone is based on illumination in terms

of lux, (L) or meter candle. The former standard foot-candle (ft-c) equals 10.764 L, and by standard agreement, the lux is now the accepted unit for expressing light intensity. The standard unit of irradiance is the langley, which is one gram calorie per square cm per second (Reifsnyder and Lull 1965).

Light intensity varies with conditions of the environment, as well as with season and time of day. Latitudinal variations in the sun, its position throughout the day, atmospheric suspended particles, vegetation, and topography affect the intensity of light received. At high elevations, about 10,000 feet or more, habitats may be exposed to intensities of 129,000 L, whereas at sea level, the intensity may be closer to 100,000 L (Daubenmire 1959). Thus, in any habitat, light intensity fluctuates hourly with changes in the position of the sun, leaf movements by wind, relative humidity changes, shadows, and other local obstructions.

Under natural conditions, light intensity should not be a limiting factor on harsh sites. However, there are exceptions, as for instance, with an increase in competition, invading plants may intercept light needed for seedling growth or seed germination. With continued respiration there is a continuous dry weight decrease in plants, but this weight loss is normally balanced or exceeded by photosynthesis. The light needed for photosynthesis to equal the weight loss through respiration is called the compensation point. This point varies with different species, but generally lies in the range of about 27 to 4,200 L for higher plants (Daubenmire 1959). This range usually represents between

about 2 and 30 percent of full sunlight, but the figure for any plant is never stable, it being a fleeting variation with time. Kozlowski (1957) found that shade tolerant species have a much lower compensation point than nontolerant species. At high light intensities, the rate of photosynthesis in shade-tolerant species begins to drop off rapidly, and may fall below the compensation point. Hellmers (1963) observed that light at lower intensities is used more efficiently by Jeffry pine seedlings, but plants grow taller and faster at higher intensities. Grime (1965) observes that seedling failures under shade are invariably associated with fungal attack, and prolonged shade increases infection.

Radiation intensity influences plant structure considerably, and can have very important implications relative to survival. Low intensities stimulate height growth, top growth at the expense of root growth, and leaf area development at the expense of strength (Reifsnyder and Lull 1965). Low intensities also tend to increase susceptibility to summer drought if precipitation is deficient. This may be an important consideration in revegetation if there is a presence of taller competing plants near by, as well as steep north slopes which will restrict solar radiation. Opaque white plastic sheets under growing plants have been used to reflect radiation reaching the ground back up to the plants (U.S.D.A. 1966). It was estimated that this technique reflects 80 percent of the radiation that normally would be absorbed by the soil.

Net radiation is the primary agent responsible for evapotranspiration and snowmelt (Reifsnyder and Lull 1965). When the soil is wet, most of the radiant energy is used in soil drying and snow melting. As the

soil dries, most of the energy will be used in sensible heat exchange.
Heating of the soil surface is an important action of such energy.
Sandy soils will easily reach temperatures in excess of 160°F, well above
the thermal death point of herbaceous seedlings (Maguire 1955). Aderikhin
(1954) found that a white chalk spread on the soil surface tended to
reflect a high incidence of solar radiation, and reduce surface temperatures
as much as 20°C. When air temperatures are warm for growth, but when
soil temperatures are low enough to prevent water absorption, plants
in north-south rows will allow a higher incidence of solar radiation
to reach the soil surface and cause warmer temperatures.

Radiation Duration

Photoperiodicity has been shown to be an important environmental
clock in all regions except equatorial areas (Leopold 1964, Oosting
1956, Daubenmire 1959). With increasing north latitude, greater seasonal
variations in day length occur. Thus, light duration is primarily a
day-light phenomenon affected by latitude, season of year, and elevation
coupled with topography. Light duration is commonly studied in two
phases; total duration of light (photoperiod), and duration of a particular
quality and intensity. The most common and applicable consideration to
harsh site revegetation is total duration or photoperiod.

The impact of light duration on plant physiology is especially
noticeable in mountainous terrain. Continuous increasing light intensity
progresses from lower to higher elevations throughout the day. During
early morning hours upper slopes are the first to become illuminated,
and remain at a higher intensity throughout the day and evening than

lower elevations. This sequence has a striking effect on plant phenology and reproduction, and may be, through interaction with temperature, a principal limiting factor to plant survival.

Britten (1961) found that flowering of Trifolium repens was retarded at lower elevations in tropical latitudes, but with an increase in elevation and an advance in day length at the same latitude, flowering was promoted. Some plants are adapted to measure daylight length very closely in terms of intensity. Some long-day plants requiring 14 or more hours of light above a maximum intensity may have the flowering stimulus depressed if the intensity falls only a few L below the minimum within the 14 hour period (Bonner and Galston 1953). Olmstead (1944) found a regular sequential pattern in flowering of sideoats grama, wherein northern strains are long-day plants and southern strains are short-day plants. Thus, the length of the required photoperiod increases with increasing elevation at a given latitude. The effects of photoperiod on the flowering response has been thoroughly reviewed by Lang (1952).

NUTRIENTS

Although the main bulk of the plant is derived from carbon, hydrogen, and oxygen obtained from the atmosphere and water, most of the elements essential for plant growth are obtained from the soil. Classically, the two major groups of soil nutrients regarded as essential for plant growth are the macro- and micronutrients. The principal difference between these two groups is primarily one of plant requirement, wherein

on a qualitative basis, micronutrients are required in smaller amounts
than macronutrients. However, Gerloff (1963) stresses that it would
be well to recognize that nutrient requirements are quite variable among
different species, and among varieties within species. What is essential
for one plant may prove to be of minor importance to another. Thus,
plants native to unusual environments may be particularly adapted to
them such that the unusual environment is in reality normal for optimum
growth. In a consideration of harsh site conditions, it will thus be
necessary to consider the nutrient status of soils in terms of requirements
and deficiencies, nutrient-root interactions, nutrient ion competition,
and nutrient-environment interrelations.

Nutrient Requirements and Deficiencies

The status of soil fertility and the availability of essential
nutrients has been found to have a considerable influence on the success
of artificial revegetation of range-watersheds (Eckert and Bleak 1960,
Eckert et al. 1961, Eckert and Evans 1963, 1965, Cook 1965, Eck et al.
1965). Exposed, sparsely vegetated, mountain harsh sites are known to
be commonly deficient in several to many essential nutrients (Eckert
and Bleak 1960, Humphrey 1962). On sites supporting an exposed parent
material or deteriorated soil mantle, conditioned by extreme environ-
mental fluctuations, and subjected to excessive weathering and erosion,
an important limiting factor to plant colonization may very well be its
fertility status.

It is apparent that on native western soils, N and P are the most
limiting elements to plant growth (Cook 1965, Eckert and Bleak 1960,

Eckert and Evans 1963). Gessel (1962) has found that N is usually critically deficient in soils of the Douglas-fir region. Fertilization of wildland soils has generally shown increased plant yields, more rapid shoot growth, and earlier initiation of growth. Most nutrient studies have shown that N and P additions are very beneficial, but fertilization with other nutrients is seldom helpful if N is excluded from the fertilizer mixture (Eckert and Evans 1963, Cook 1965, Eckert et al. 1961). Micronutrient studies on wildland soils have generally yielded similar results, wherein N together with micronutrients result in no significant differences from N alone. This indicates that micronutrients are either in satisfactory quantities in native soils, or they are added with the macronutrients at the time of fertilization (Eckert et al. 1961, Bonner and Galston 1958).

Fehl and Lange (1965) found that the addition of a high-calorie C nutrient solution to soils causes a vigorous microbial growth of Fusarium sp. This results in increased soil stability, but causes rapid depletion of essential inorganic soil nutrients, and may produce phytoxic organic compounds. Bliss (1962) feels that N deficiencies in cold climates may be due to low bacterial activity resulting from low temperatures. Plants may contain high foliar quantities of N, but low temperatures inhibit assimilation of nucleo-proteins, hence producing N deficiencies. Water derived from snow is nearly free of solutes, and may also contribute to low quantities of elements. Shields and Durrell (1964) found soils that support an active colony of algae or lichen have N levels about five times greater than where these organisms are absent.

A thorough review of the physiological processes influenced by each nutrient element, and the growth and development stages to which each pertains is beyond the scope of this paper, but complete discussions are available (Gauch 1957, Brown 1963, Gerloff 1963, Leopold 1964). However, a brief summary of those which are most pertinent to wildland plants on harsh sites is warranted, especially in view of Billings (1957) statement that more intensive nutrition studies relative to wildland native plants are needed. Daubenmire (1959) indicates that flower production and sex expression in plants is strongly influenced by the relative availability of essential nutrients. Although no known K-containing compounds are found in plants, Gauch (1957) feels that the high concentration of K needed is explained on this basis. On mountain-range sites recently invaded by coniferous forests, the deposition of acid-forming litter causes an increase in soil pH and a loss through leaching of nutrient bases. Wallace (1965) discusses the possibilities of using chelating agents for increasing the availability of metal ions. In some cases the addition of Ca may enhance the uptake of other-wise unavailable nutrients. Certain plants have natural chelating agents which are released as a product of respiration, usually chemically similar to malic and malonic acids (Gerloff 1963). Gauch (1957) indicates that ion deficiencies may result in respiration reductions, wherein the seriousness of this condition can be considerable, as with B deficiencies which cause internal sugar deficiencies.

The establishment of a protective plant cover on harsh sites will require a thorough knowledge of the nutrient requirements and deficiency

symptoms of the particular species involved. Physiological tolerance limits and requirements studies will help to establish limits within which optimum growth can be expected for species selected for revegetation.

Soil-Plant Root Interactions

Nutrient ions may enter plant roots by one of two ways; by diffusion or passive adsorption, or by the action of carriers through active absorption (Gauch 1957). Relative to the passive adsorption process, ions are adsorbed non-metabolically by negatively charged surfaces within the root. Relative to the carrier or active absorption process, ions are combined with carriers chemically in the soil medium, and the ion-carrier complexes traverse membranes of limited permeability.

There appears to be considerable disagreement among plant physiologists as to which of the two modes of ion entry are most important. It is well established that plant roots, like soils, have cation exchange properties (Brown 1963). Roots act as amphoteric colloids and adsorb cations from the surrounding medium on a rather non-specific basis in the "outer space" of cells. Plant root cation exchange capacity (C.E.C.) may exert a quantitative influence on nutrient uptake in a medium of low ionic activity by raising the concentration of cations at the root surface above the level in the surrounding solution, and by influencing the relative proportions of ions of different valency at the root surface. The importance of soil-plant root relations may have profound implications relative to competition between species. On sites where nutrients are in low levels of availability, presumably those species with a higher C.E.C. will more effectively be able to adsorb needed elements. In this

respect, Gauch (1957) feels that compatibility of different species
is positively correlated with the C.E.C. of their root systems. This
is amplified by the fact that cation uptake depends upon the relative
exchange capacities of the root and soil. Gauch (1957) quotes evidence
indicating that dicots have nearly twice the C.E.C. of monocots, and
Brown (1963) indicates that on a relative scale of C.E.C., legumes >
herbs > grasses. However, on the basis of this evidence, it is difficult
to understand the capacity of most grasses to grow on harsh sites of
low fertility.

Metabolic ion absorption, or active absorption, is selective in
nature, and causes a certain amount of energy expenditure on the part
of the plant. It has been variously noted that growing plants seldom
absorb the various ions in the proportion in which the ions are present
in the soil. Rather, they exert a selective action, absorbing greater
proportions of some ions than others, depending upon the plant and
environmental conditions. Through the action of ribonucleoprotein
carriers, whereby nucleic acid binds cations and protein moiety binds
anions, ions are released free into the cell vacuole during protein
synthesis. There is still considerable controversy about this hypothesis.
Evidence indicates however, that entry of solutes into the plant is
metabolically regulated and does not occur freely in significant amounts
(Gauch 1957, Leopold 1964, Brown 1963). Perhaps ion entry is accomplished
through both passive and active processes, whereby ions are accumulated
on the charged sites of roots, and actively absorbed by carriers into
cell vacuoles. The mechanism of ion uptake by plants, by whatever mode

of transport, is profoundly important to plant survival on harsh sites
because of the phenomena of ion competition and environmental restric-
tions on absorption.

Nutrient Element Competition

There is an abundance of evidence indicating that, under certain
circumstances, a high degree of competition or antagonism exists among
ions. Certain ions are more successful competitors for binding sites
in plant cells than others, with the result that chlorosis or toxicity
relative to certain ions insues (Wallace 1965, Brown 1963, Gauch 1957).
Competition for absorption involves the relative abundance of ions,
the combining power of ions, the selective absorptive capacity of roots,
the solubility factors in the soil, and the translocation process from
the root to the top of the plant. There are striking differences among
plant species in their capacity to absorb specific ions from a growth
medium, which emphasizes the principle that nutrient requirements for
all species are not the same, and that for any one species, they will
vary with conditions of the surrounding soil medium (Gerloff 1963).

Perhaps the most striking phenomena relative to ion competition is
the effect of the $H+$ ion in soils of low pH on the availability of other
ions. Besides the purely physical basis of electrical charge for ion
selectivity, there is also a chemical basis for ion absorption. In
soils with a low pH, the addition of Ca creates a chemical antagonism
whereby the Ca competes with metal ions of Fe and Zn. The same effect
has been described for P and other cations (Gerloff 1963, Wallace 1965).
The availability in the soil of many of the essential elements is closely

correlated with pH. Even at pH values as low as 4.5, it seems likely
that poor plant growth does not result directly from the injurious
effects of the H ion but indirectly from the toxicity of metals or from
the reduced availability of one or more elements (Gerloff 1963).

The concept of ion competition and interactions is too broad to
be covered here, but its implications relative to harsh site rehabilita-
tion are obvious. It must be recognized that plants adapted to unusual
environments may have specific requirements for certain elements that,
under natural conditions, cannot be supplied if that plant is introduced
into habitats other than those commensurate with its physiological
requirements. This may have some rather far reaching implications,
wherein the effects of ion interactions should be considered. The
minimum amount of an element necessary for maximum growth is not an
absolute value but depends upon the relative amounts of other elements
available. The effects of high H+ concentration, the inactivation of
P by Al, the antagonism of Ca for Fe and other minor metals, the require-
ment of Ca for NO_3 and K uptake, the effects of P on the accentuation
of both Zn and Fe deficiencies, and the effect of P on increasing Mg
deficiencies are good examples.

Nutrient Element Interactions with Environment

Chlorosis resulting from deficiencies of various ions is frequently
perpetuated and encouraged by environmental conditions. Wallace (1965)
has suggested that iron chlorosis may very well be correlated with exces-
sive high or low soil temperatures, unusual moisture conditions, or even
sometimes direct sunlight. Billings (1957) has suggested that strong

endemism may result from local climatic and environmental effects on
the nutritional status of soils. For Utah, Peterson and Smith (1964)
suggest that Ge deficiencies occur where soils are kept moist to wet,
and Zn deficiencies occur primarily during cold wet spring weather,
especially on sandy soils.

The effect of environmental factor fluctuations may be responsible
for rather extensive variations of nutrient availability on harsh sites.
However, climatic and environmental characterization studies of harsh
sites are critically limited, let alone studies of nutrient ion availa-
bility. Haupt (1956) found that N content of granitic soils was reduced
about 11 percent following a single average summer rainstorm. Average
N content is also reduced by trampling disturbance and increased plant
cover. Timm et al. (1966) found with potato and sorghum plants that
micronutrient deficiencies of Mn and Fe show up as symptoms following
periods of high temperatures over $90^{\circ}F$, but when temperature drops to
$80^{\circ}F$ new growth is normal. They feel that this is due to a period of
rapid growth under warm conditions, and that nutrients cannot be supplied
at an optimum rate. Aderikhin (1954) found that in darker warmer soils,
the content of NO_3 and P is much higher than in lighter cooler soils.
Power et al. (1963) found an increase in available P widened the soil
temperature range over which maximum growth occurs. At intermediate
or low levels of P available for barley growth, temperatures slightly
above or below optimum greatly restricted growth. Pellet and Roberts
(1963) found that a high N level in the tissues of Kentucky bluegrass
lowered its resistance to high temperatures. Combinations of high K

and N increased the resistance to high temperatures. Stone and Will

(1965) indicate that B deficiencies are purely seasonal for Pinus radiata

and P. pinaster, usually becoming prominant in midsummer. A correlation

between summer drought and B deficiencies is not strongly substantiated.

Gessel (1962) quotes studies that show that available P increases can

be expected following forest fires in the Douglas-fir region of the

Pacific Northwest. Kozlowski (1964) cites numerous examples whereby

moisture deficits alter N metabolism. Other studies have shown that P,

K, and Mg are highest in plants grown under favorable moisture conditions.

Long, recurrent droughts apparently restrict the availability of many

essential macro- and micronutrients in the soil.

It can be easily seen, then, that the relative availability of

nutrient ions can be greatly affected by environmental conditions, and

that relative proportions of ions have important modifying characteristics

on environmental factors. These principles may have far-reaching effects

on revegetation attempts of harsh sites, and obviously must be considered

closely. For instance, Power et al. (1963) suggest the possibility of

maintaining a high level of P in soils that are likely to witness adverse

extremes in temperature for crop protection. The possibility of thus

chemically modifying limiting environmental factors is interesting,

and worthy of more intensive study.

COMPETITION

Unlike all other environmental factors, competition encompasses

both the physical and biological facets of the biosphere. Competition

is an expression of the interactions between species and individuals
that have the same or similar requirements for growth and survival.
As a concept, competition usually implies situations of negative influ-
ences due to physiological stress as the result of a lack or shortage
of some requirement. However, this implication can be extended beyond
to include other types of reciprocal effects such as the secretion of
harmful or toxic substances. The competitive interaction may involve
common space, water, light, nutrients, temperature effects, disease
resistance, mutual predation, and many others. Competition may result
in equilibrium adjustments by two species or among many species as an
expression of dominance, or it can result in one species population
replacing another.

The ubiquitous nature of competition is prevalent wherever two or
more organisms exist in the same environment. The more closely related
are the requirements among individuals or species, or the more similar
are their ecological niches, the more critical their competitive ability
becomes. The intensity of competition is a measure of how much the
supply exceeds the demand. The competitive ability of the plant is a
manifestation of its adaptability to the site, and may vary with age
and stage of development. Through continuous interaction, there may
result a condition of relative stability and an expression of single
or multiple species dominance.

Plants introduced into harsh site environments will be competitively
influenced by three principal facets: (1) the effects of limiting
environmental factors, (2) the effects of toxic substances from other
plants, and (3) plant-animal interactions, such as from grazing.

Effects of Limiting Factors

A physiological expression of environmental stress indicates a deficiency in some factor. A deficient factor may result because the site is physically incapable of supply, or it may result due to competition. This principle is of such basic importance to any consideration of artificial revegetation that its implications can mean the difference between success and complete failure (Plummer et al. 1955). An introduced species may be fully capable of sustaining optimum physiological activity on a particular site, but survival may be impossible because of competition. One of the primary concerns in artificial revegetation is to provide an environment commensurate with the limits of survival of the introduced plant. Closed communities of established stands that fully utilize the habitat are not readily invaded, either naturally or artificially (Robertson and Pearse 1945). Without an adequate opening of the community by some external means, the invasion and establishment of introduced species is practically impossible.

In the majority of instances, either interspecific or intraspecific competition leads to a situation of negative correlation among competing members. Competition between members of a single species is usually much more intense than among members of different species. Individuals of a single species all mature about the same time, roots utilize moisture from the same layers, and they compete for light at about the same level (Humphrey 1962, Kershaw 1964). Where a variety of species is represented, as is the most usual case in nature, competition intensity of any one species may not be as great, and in fact, mutualism may be beneficial.

Where phenological events progress at different times for different
species, the demands made on the environment are not as pressing.
Thus, requirements for quantities of environmental factors vary during
the season among species for germination, emergence, growth, flowering,
and seed set. In this sense, mixtures of species for seeding have
been widely recommended (Humphrey 1962, Robertson and Pearse 1945,
Schultz and Biswell 1952, Stoddart 1946, Stoddart and Smith 1955).

Perhaps the most common competition effect on plant establishment,
survival, and ultimate community species composition is the direct
negative stress effect of competition. A species adapted to the fullest
utilization of the most limiting factor in the environment will have
the greatest competition advantage, and will most successfully maintain
its presence in the environment. Under natural conditions, soil water
appears to be the single most important factor limiting to successful
plant establishment and is that factor usually in greatest demand by
competing plants. Cook et al. (1965) concluded that grass and rabbit-
brush compete for soil moisture during the spring and summer growing
season. Rabbitbrush utilizes moisture that otherwise would be available
to grasses, consequently retarding the potential production of desirable
species. Blaisdell (1949) found that grasses established before sagebrush
invasion are capable of retarding sagebrush introduction into the stand
due to the more efficient and complete use of moisture by grasses.
Seeding rates in excess of the potential of the site will produce a
profusion of seedlings which may deplete optimum moisture conditions

to the point where mature plants cannot survive (Humphrey 1962). Kozlowski (1964) cites evidence indicating that root development in ponderosa pine is about three times greater when grown free of competition. Rooting habits of shrubs and some herbaceous species are frequently aggressive enough to preclude maximum development of desirable species. Certain species such as sagebrush and cheatgrass, are adapted to rooting habits that permit extraction of soil moisture more efficiently than many native species (Cook and Lewis 1963, Robertson and Pearse 1945, Frischknecht 1963, Hopkins 1953, Everson 1951, Mueggler and Blaisdell 1951, Hedrick et al. 1964, Tabler 1964). Stewart and Hull (1949) discuss in detail the extensive competitive ability of cheatgrass.

A plant's competitive ability quite often varies with its age and stage of development. In most instances a plant becomes more competitive with older age, seedlings being the most susceptible to competition exclusion. Blaisdell (1949) found that grass seedlings established one year before sagebrush invasion yield a much higher forage production than sagebrush plants. Seeding into established sagebrush stands, even those only one year old, will suppress grass growth and production. Perennial grass seedlings are poor competitors with an annual profuse seeder like cheatgrass. Stewart and Hull (1949) showed that cheatgrass potentially can produce over 1600 seedlings per square foot. Cheatgrass is a severe competitor and can successfully retard perennial plant invasion, but is able to invade perennial stands during periods of extended drought or disturbance (Robertson and Pearse 1945). Hull (1963) showed that the rapid growth of cheatgrass, when

grown together with wheatgrass seedlings, enables it to extend a deeper root system, and retard wheatgrass growth from 1/7 to 1/3 of that under no competition.

With an increase in age and maturation development, adapted perennial species are better equipped to utilize the habitat and form a closed system to invasion. Mueggler and Blaisdell (1951) found that with the successful eradication of wyethia, seeded perennial grasses are able to occupy the site and prevent the reinvasion of the undesirable plant. Blaisdell (1949) indicates that a good stand of mature perennial grasses will suppress sagebrush invasion for an indefinite period if grazing is controlled and extensive drought is averted. Besides age, life-form and a perennial or annual growth form are also important. Hopkins (1953) found that mid-grasses have an advantage over shortgrasses in occupying a site, principally because of a more extensive and rapid root growth rate. Schultz and Biswell (1952) found that annual ryegrass has a profuse seeding rate capable of suppressing the yield of perennial grasses. Similar results have been indicated in studies with cheatgrass and other annuals (Robertson and Pearse 1945, Stewart and Hull 1949, Hull 1963).

Dominance of a species in a stand is usually associated with superior competitive ability. Whittaker (1965) feels success in competition leads to dominance, and is best expressed in terms of productivity. Through stratification, a species may assume a dominant role, in that it maintains control of the environmental factors on the site. There is conflict between the concepts of dominance and tolerance relative

to competition. A species is able to survive under domination because its physiological requirements are different in some respects from the dominant. Tolerant species are usually the understory members of a stand stratum. However, true dominance involves the ability to compete successfully in all strata. This has been shown to be characteristic of many undesirable species encountered on western rangelands, such as sagebrush (Blaisdell 1949), cheatgrass (Stewart and Hull 1949, Robertson and Pearse 1945), wyethia (Mueggler and Blaisdell 1951), and rabbitbrush (Cook et al. 1965, Frischknecht 1963).

Understory tolerant species are often detrimental to optimum growth and development of overstory species. Hedrick et al. (1964) found that overstory grass production was highest where understory species had been eliminated. Growth studies indicated the competitive ability of species in association with other species. Crested wheatgrass was found to have the highest competitive ability, and big bluegrass the least.

Effect of Toxic Substances

Certain species may secrete toxic substances that inhibit plant growth. There is little doubt that certain plants have an inhibitory effect either on others of the same species or on those of different species. Humphrey (1962) cites evidence indicating that in soils containing dead bromegrass roots, when seeded to the same species, production of smaller shoot and root yields result than in soils free of these roots. Another plant, Artemisia absinthium, bears glandular hairs that secrete ethereal oils and the alkaloid, absinthium. Absinthium is washed from the leaves and incorporated into the soil, and causes

an inhibition to growth of other species. Billings (1957) points out
that many species may secrete toxic substances limiting to plant growth.
Horseweed has been found to produce a substance that is toxic to itself,
and thus is an important factor in the short-term occupancy of this
plant on abandoned and disturbed sites. The living rhizomes of quack
grass have been shown to inhibit the germination and growth of seedlings
of most weedy species, but promote the emergence of some.

These, then, are examples of actual biostatic inhibition, but the
phenomenon appears to be rare among the higher plants. However, as
Billings (1957) points out, it may appear rare only because of lack
of data to show it. Radioactive tracers have been used to show that
certain elements may be carried through the roots of one plant and
appear in the tissues of another. It is conceivable that organic toxins,
growth substances, or toxic ions could be carried and released by the
roots of certain plants in the same manner.

Plant and Animal Interactions

The effects of animal activities on the normal physiological processes
of plants have been widely studied, particularly the effects of the
grazing animal. Continuous heavy grazing pressure tends to weaken those
preferred species, primarily through reduction of plant food reserves,
removal of floral primordia, removal of leaves and other photosynthetic
material, and interruption of the photoperiodic stimulus. The two most
important factors affecting the grazing resistance of a species are:
(1) height of the growing point above the ground level, and (2) the ratio
of fertile to vegetative stems. It is primarily the effect of these

two factors that determines the "decreaser-increaser" principle of range
management (Branson 1953). The highly selective nature of the grazing
animal, either domestic or wild, elevates it as the greatest concern
in the management of artificially revegetated stands.

There have been some rather good recent studies and reviews on
the effects of biotic influences on plant physiological processes.
Jameson (1963) reviewed a large volume of literature on the effects of
harvesting on responses of individual plants, and has come to the
following conclusions: (1) most often removal of herbage reduces dry
matter production, (2) legumes are more resistant to grazing than grasses,
grasses more than other forbs, and shrubs more resistant in terms of
current season growth, (3) tillering is stimulated by removal of the
growing point, (4) morphological changes may occur resulting from
grazing, (5) seed yields are often reduced, (6) root weights and growth
are generally decreased, (7) carbohydrate reserves in the roots are
decreased, some of which may be required for herbage production, (8)
reduced root growth and carbohydrate reserves result in reduced top
growth. Ellison (1960) concludes that grazing is somewhat similar
to parasitism by the animals on the plants. He points out many of the
same conclusions mentioned above in terms of the detrimental effects of
grazing on the physiological activities of the plant. Packer (1953)
has shown the effects of trampling on watershed condition, runoff, and
erosion. On both wheatgrass and cheatgrass ranges, a 20 percent trampling
disturbance increased overland flow and soil erosion beyond established
safe maximum amounts.

Besides the grazing and browsing animals, insects, birds, squirrels, mice, and other rodents often grossly affect the physiology of plants. Large quantities of photosynthetic material and seeds are consumed seasonally by these animals. Also, protoza, nematodes, mites, earthworms, and burrowing vertebrates rate further study of their effects on plant physiological activities.

PLANT PHYSIOLOGY STUDIES NEEDED

It has been fairly well established that under natural circum-
stances water availability and temperature conditions in the immediate
microenvironment of plants are the most important variables controlling
survival. As basic environmental factors, water and temperature are
inseparably related to the vital processes of metabolism and growth
through protoplasm production and chemosynthetic reactions. However,
the implication should not be made that factors of radiant energy,
nutrition, and biological competition are any less important to the
basic physiology of the plant. Under natural conditions, however,
the latter three factors do not appear to be principal limiting ingredients
to plant establishment and survival. The literature bears this point
out, wherein the success or failure of revegetation attempts is deter-
mined primarily on the basis of water availability and temperature
extremes. Competition may be considered a primary limiting factor,
but the effects of competition usually reflect a deficit in the availa-
bility of water.

The preceding literature review reveals that much of the basic
physiological information needed for plant establishment on harsh sites
is lacking. Several rather conspicuous facts are brought into focus
from this review. First, the overwhelming majority of research efforts
on the physiological responses of plants are primarily of a theoretical
nature, wherein they do not carry to a logical conclusion the effects

of a highly complex and variable environment on the survival and growth of the plant. Second, remarkably few intensive and basic physiological studies have been conducted with wildland species, especially those used for artificial revegetation. It appears that the views of Storey (1960) and Billings (1957) are well founded, wherein land managers frequently, and perhaps conveniently, overlook the fact that the plant is the primary agent through which management is carried out. As a result, strikingly little is really known about them. Third, how can we ever hope to understand the complex interrelations between plants and environment if our knowledge of physiological responses is based on empirical qualitative methods and observations?

A second important consideration to be made is that of the minimal, optimal, and maximal intensities of environmental factors relative to physiological tolerance limits. The particular range of any one factor is not fixed, but varies with other conditions in the habitat. This places a severe limitation on extrapolation of data from studies where all factors are held constant but one. The effect of a particular factor at a given intensity on the physiological processes of a plant may be quite different as all other factors change. Also, as the plant individual grows from the seed stage to seedling, and then maturity, the entire complex of interacting factors affect it with different magnitudes and intensities. It is obviously important to know that if a site is capable of supporting a mature plant of a species, that it will also support the processes of seed germination and seedling survival. Thus, the real problem becomes one of determining for each species, and

perhaps for each of its selected ecotypes, what environmental factors
are most limiting to its survival at various stages of growth, and
to what intensity they are affected by various combinations of factor
interactions.

The remaining sections of this problem analysis will outline
specific physiological studies required to gain basic knowledge of
the physiological tolerance limits of plants.

PHYSIOLOGICAL TOLERANCE LIMITS STUDIES

Studies Under Controlled Laboratory Conditions

Water - Studies are needed to determine primarily the effects
of plant water stress on survival and growth. We must understand the
relationships between internal plant water balance and soil water
stress, and their effects on basic physiological processes. These
should involve variables of water amount, duration of stress, and the
effects of replenishment on growth stages of seed germination, seedling
survival by age, and metabolism and reproduction in mature plants.
Studies are also needed concerning the effects of drying on moisture
depth in soil, and the rate of root growth of young seedlings relative
to rate of drying. In these studies water availability is the principal
variable, while other factors should be held constant. However, studies
are also needed wherein the effects of environmental factor interactions
are incorporated, such as temperature effects, light intensity effects,
and nutrition levels. Also, the effects of various degrees of plant
competition intensity, either by other species of the same or different

life-form, or between members of the same species, on water availability
are needed.

Temperature - Wide variations in extremes of temperature exert
important stresses on plant physiological processes. As a single-
factor study, the effects of low and high temperature stress should
be studied on seed germination, seedling growth and survival, and mature
plant metabolism and reproduction. These studies should include both
air temperature extreme effects and soil temperature effects. The modifying
effects of water availability, wind speed and duration, nutrition levels
and plant competition on temperatures, and the consequent effects on
plant physiological processes should also be studied.

Light - Light, or total solar radiation, effects are seldom a
direct limiting single factor to physiology under natural conditions.
However, as light quality, duration, and intensity are affected by the
presence of other plants through competition, as a competitive factor,
it may be a direct limiting factor. The effects of light should be
studied principally in terms of how it is affected by competition, and
its interacting effects with temperature, water, and nutrition stress.

Nutrition - Studies are needed to determine the effects of various
macronutrient deficiencies on seed germination, seedling growth and
survival, and mature plant metabolism and reproduction. It has generally
been found that micronutrients are not lacking under natural conditions,
but this may require further investigation before it can be eliminated
as a limiting factor. Interactions with other variables of water supply,
temperature extremes, light effects, and competition intensity with

various levels of soil nutrients needs to be studied. Methods of
studying nutrient levels under controlled conditions have been exten-
sively developed, wherein glass or plastic pots containing the medium
for plant growth are used. Use of standard nutrient solutions and
fertilizers containing N, P, and K, and possibly other elements, can
easily be obtained for such studies.

Competition - Aside from studies of competition effects on environ-
mental factors among species and individuals of the same species, studies
are needed to determine the effects of soil microorganisms on the growth
stages of germination, seedling survival, and growth of mature plants.
Fungal infections of such species as Podosporiella verticillata appear
to be common throughout the Intermountain Region. This may require
special microbiological methods and techniques not immediately available
to our research staff, but the importance of this factor should not be
underrated. It may be found necessary to also study the effect, and
methods of control, of various species of snow molds on seeds and germin-
ation. Also, further studies may be required to determine the effects
on physiological processes of specific species of various degrees of
trampling and grazing. Although the principal objective of harsh site
revegetation will be to provide a protective plant cover for erosion
control, some management system may have to be employed to protect
young seedlings and the intensity of plant removal.

Studies Under Field Conditions

A rather unusual opportunity for detailed study of plant physio-
logical processes in the field may present itself in the near future

when harsh site microenvironmental characterization studies are begun.

Advantage of such a rare opportunity should certainly be taken. Under

these conditions, detailed study of the entire spectrum of microenviron-

mental conditions at specific harsh site habitats strategically located

throughout the Intermountain Station territory will be undertaken. It

is proposed that at each of these harsh site habitats, physiological

studies be conducted with selected species in close conjunction with

both microenvironmental and revegetation techniques studies. Although

environmental conditions at these sites cannot be controlled, they will

be accurately monitored in such manner as to permit close study of

plant physiological processes as influenced by the microenvironment.

This approach, together with revegetation techniques studies, all

coupled directly or indirectly with the microenvironmental study, should

help to clarify the close interrelations and associations shared by each

of these research endeavors. Under certain conditions, field studies

of plant physiological tolerance limits and responses to environmental

conditions, and studies of revegetation techniques will be conducted

simultaneously at the same locations. The physiological studies to be

confined to the laboratory will form the basis for field studies to be

conducted under harsh site conditions. Field physiological studies

should facilitate bridging the gap between purely basic research and

more applied research on revegetation techniques. Thus, the subject

matter and specific studies outlined in the problem analysis on revegetation

techniques will be a direct extension of the studies proposed here, and

the two should be considered related and inseparable. Therefore,

laboratory and field studies will not be antagonistic, but rather complimentary to each other.

Cooperation between Projects 1603 and 1704 has been extensively discussed among project scientists conducting physiological research. It is apparent that many of the studies proposed here are also planned by Project 1704. Relative to the personnel of Project 1603 and any conflict that may arise between field and laboratory work, laboratory physiological studies are adaptable to a very flexible schedule during any season of the year. Field physiology studies may be conducted usually only during periods of favorable weather, whereas, laboratory studies may be conducted during any season. Also, through cooperation with personnel of other projects, it may prove possible to conduct both types of research simultaneously.

PLANT BREEDING AND INTRODUCTION

Through studies and programs of breeding native and introduced hybrids, as well as introduced species of plants from other countries and areas of this country, it may be possible to provide a broader pool of adapted species for use in revegetation of harsh sites.

Studies are needed that will attempt to determine what favorable tolerance and growth characteristics exist in native and introduced species which will enhance their survival and effectiveness as a protective cover on harsh sites. It would then be possible to manifest these desirable traits through selective breeding, and then harvesting of viable seed in other plant materials to be used for revegetation.

Harlan (1951) points out that many revegetation failures can be attributed to a failure to recognize varietal differences in both native and introduced species. Often the differences in adaptation between strains of a species are greater than differences between species, and provisions for recognition of these differences should be provided. Tisdale (1962) has observed that interest in plant breeding and strain selection is growing rapidly because of its value in allowing selection of superior strains for revegetation. Ecotype variation among native species has long been recognized as a key to local adaptation to particular environmental conditions (Hergen 1963, Peacock and McMillan 1965, Passey and Hugie 1963). Recognition and distinction of particular ecotypes of a species are commonly determined through common-garden plots, which also permit recognition of superior characters for particular environments. This same procedure has been applied to introduced species, such as crested wheatgrass and medusahead (Dewey 1962, McKell et al. 1962).

An active program of maintaining correspondence with workers concerned with revegetation in other countries and areas of the U. S. has been initiated by the author during late 1965. Through this program it is hoped that plant materials can be obtained, through proper channels of customs and quarantine, that show promise as revegetation species in the Intermountain Region. By no means have the sources of potentially valuable introduced species been exhausted, and it is certain that many more species remain to be critically studied as potential plants for revegetation. Ruf and Farmer (1964) have proposed just such a study, and are presently engaged in outplanting studies with squaw carpet

(Ceanothus prostratus), a native of the Sierra Nevada, in various places in the West, including Utah. The author has obtained seed of Penngift crownvetch (Coronilla varia), a legume of considerable importance for its wide use as an erosion control plant in the eastern U. S. Plants are currently being grown in the greenhouse, and studies will be undertaken soon to determine its value for erosion control in the West. The author has maintained contact with M. J. Wraight, a forest scientist in New Zealand Forest Service, in response to his paper (Wraight 1965) concerning the potential growth rates of alpine carpet grass. Subsequent correspondence has yielded that besides carpet grass, Notodanthonia setifolia may also be potentially advantageous to revegetation of particularly critical small areas in the Intermountain Region. The environment of the native habitats of these two species is quite similar to those environments of high elevation harsh sites here in the Intermountain Region. Contacts with the Plant Introduction and Plant Materials Divisions of the ARS in both Pullman, Washington, and Beltsville, Maryland have also been made. These contacts may especially prove to be valuable. They have agreed to arrange for the quarantine and customs procedures for the shipment of plant materials of the above two species into the U. S. from New Zealand.

It is suggested that this program be continued, and perhaps expanded in an effect to discover promising species for revegetation of high elevation harsh sites.

PROPOSED PROGRAM OF RESEARCH

The objective of this proposed program of research is to provide a framework upon which the following may be determined:

1. Determine the physiological tolerance limits of selected plant species in terms of the environmental factors characteristic of harsh sites that are limiting to plant growth and survival.

2. Provide a basis upon which species or species varieties can be accepted or rejected for revegetation of harsh sites with known microenvironmental characteristics.

3. Provide basic physiological information concerning selected species in such terms as it can be extended to field trials of on-site adaptation studies.

The areas selected for specific study as outlined in this proposed program are drawn from the literature as representing those problems that appear to be most limiting to successful artificial establishment of plants on natural harsh sites. The studies proposed here are principally basic in character, and are to be conducted under precisely controlled laboratory conditions and monitored environmental field conditions.

The study prospectuses proposed below are designed to provide basic quantitative information concerning plant physiological processes in relation to those environmental factors considered to be most influential under harsh site conditions. Sufficient flexibility has been incorporated into this proposed program of research to permit each prospectus to be treated as a single study, or where needed, as more than one study.

PROSPECTUSES

A list of proposed studies is presented below in terms of study titles and their respective priorities. Priorities have been assigned on the basis of the importance of each study relative to how its subject matter applies to limiting factors of plant growth. Thus, priority categories have been broken down into three major classes, including "A", "B", and "C". The "A"-class indicates those studies requiring immediate attention, and that deal with those factors most limiting to plant survival and growth, whereas those in class "B" are of intermediate importance, and those in "C" are of least importance. Also, within each class, sub-categories labeled 1, 2, 3, . . . etc., have been deliniated on the basis of importance, wherein a study labeled A1 is of some degree more urgent than one labeled A2. Following this list are more detailed prospectuses for each proposed study.

Study Title	Priority
1. The effects of soil water stress on plant growth and survival relative to stage of development, and consequent effects on plant internal water balance.	A1
2. The effects of air and soil temperature extremes on the survival and growth of plant species, and the interacting effects of temperature on soil water availability and internal water balance.	A2
3. The effects of wind as an influence on soil water content, internal water balance, and plant-air temperatures in relation to plant growth and survival.	B1

Study Title	Priority

4. The effects of inter- and intraspecific competition intensity on soil-water-plant relations, and its effect on plant growth rate, development, and survival. **B2**

5. The nutrient requirements of plants and the effects of elemental competition and environmental factor interactions on the survival and growth of selected species. **B3**

6. The influence of inter- and intraspecific competition intensity on radiation intensity, quality, and duration, and its effect on the survival and growth of selected species. **B4**

7. Methods of breaking bud and seed dormancy, and the effects of environmental stress on germination and bud growth for plant species selected for revegetation. **C1**

8. The effects of growth regulators on the survival and growth of plant species selected for revegetation. **C2**

Priority A1

Study Title: The effects of soil water stress on plant growth and
survival relative to stage of development, and consequent effects on
plant internal water balance.

Objectives: To determine the quantitative effects of soil moisture
stress on plant growth, development, and survival, and to determine the
relationship between soil water stress and internal water stress in the
plant. To determine the stress level at which permanent wilting occurs,
and to determine by age and stage of development the growth responses to
various levels of water stress. To determine the rate of water use under
various environmental conditions in the laboratory and in the field.

Justification: There is overwhelming evidence indicating that plants
respond differently at various ages to different levels of water stress.
A quantitative expression of these effects for selected species would
facilitate an understanding of species adaptation to particular site
conditions of moisture variability. Also, the level of soil water stress
is in no way a measure of plant water stress, and hence is not an
indicator of physiological water balance. Plant water stress is controlled
indirectly by soil water, and directly by atmospheric conditions. There-
fore, rates of transpiration under various environmental conditions on
harsh sites will allow for the evaluation of water use with growth.

Study Methods: Soil water tensions will be maintained employing the
principle of water diffusion from areas of high free energy to regions
of low free energy through porous semipermeable media from an adjusted
osmoticum to a soil mass in a growth cell. Under field conditions this
may also be done using plant phytometers and maintaining given water
contents through frequent weighings. Internal water balance will be
determined with the vapor pressure method, using either the electric
hygrometer or probe. Continuous monitoring of transpiration will be
accomplished with either coil induction or strain gages connected to
recorders. All water use values will be expressed in terms of transpiring
surface area.

Time Requirement: Four years.

Location: Forestry Sciences Laboratory, Logan, Utah, and various field
locations to be chosen.

Personnel: Brown and one technician.

Priority A2

Study Title: The effects of air and soil temperature extremes on the
survival and growth of plant species, and the interacting effects of
temperature on soil water availability and internal water balance.

Objectives: To determine the effects of air and soil temperature extremes
on plants physiological processes and growth at various ages beyond
germination, and to determine the effects of various temperature and
humidity extremes on the rate of soil water depletion and plant transpir-
ation rates and internal water stress fluctuations.

Justification: Air and soil temperatures at high elevations, due to a
high incidence of solar radiation, have been shown to approach extreme
values for physiological processes. Soil surface temperatures in excess
of 150°F have been recorded, and air temperatures near the ground above
100°F are common. These extreme temperatures are known to increase the
rate of water use by plants, and accelerate the depletion of soil water.
Plant responses are known to vary with age over wide temperature fluctua-
tions, and a determination of those age levels most susceptible to injury
will aid in developing revegetation techniques suitable for harsh site
conditions.

Study Methods: This will be primarily a laboratory study, although not
entirely exclusive of field study, and will require the use of precise
environmental growth chambers. Plants of various ages in phytometers
will be grown under various temperature-stress conditions, and rate of
growth, survival, and rate of soil water and plant water depletion will
be determined. Soil temperature effects on growth and survival, as well
as on soil water depletion, will be achieved using infrared lamps to heat
soil surfaces. Plant surface temperatures will be determined with
thermocouples. Both high and low temperature effects will be evaluated.

Time Requirement: Two years.

Location: Forestry Sciences Laboratory, Logan, Utah, and various field
locations to be chosen.

Personnel: One professional and one technician.

Priority B1

Study Title: The effects of wind as an influence on soil water content, internal water balance of plants, and plant-air temperatures in relation to plant growth and survival.

Objectives: To determine the effects of wind, under various speeds and duration, on the rate of soil drying and depth of drying, and to determine its effects on the rate of transpiration and fluctuations of the internal water balance of plants in terms of various soil water conditions. Also, to determine its effects on temperature gradients between plant surfaces and free moving air.

Justification: More research is needed to evaluate the responses of various species to stress conditions imposed by wind. It is well known that one of the more critical factors of harsh sites relative to plant survival is the persistence and velocity of drying winds. Wind causes rapid increases in the rate of plant water use, and places severe strains on the available soil water. Very slight winds are enough to disrupt the vapor pressure gradient equilibrium existing at the plant surface-atmosphere interface to the extent that transpiration is doubled. Thus, a site may be capable of supporting a protective plant cover, but because of wind, the resulting interactions create a lethal environmental deficiency.

Study Methods: This study will require the construction of a wind tunnel for the precise control of wind speed and air temperature. Plants of each selected species at various ages will be subjected to various wind speeds for various durations, and determinations in growth, structural form, and survival will be made. Under these same conditions, wind effects on rate of soil drying, and depth of drying, under various soil-water contents will be determined. Continuous monitoring of transpiration through recorders will be used to determine transpiration rate fluctuations under varying wind conditions. Probes will be used to determine fluctuations in the internal water balance of plants, and this will be correlated with growth and survival. Thermocouples will be used to determine the differences in plant and air temperatures under various wind conditions.

Time Requirement: Two years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

Priority B2

Study Title: The effects of inter- and intraspecific competition intensity
on soil-water-plant relations, and its effect on plant growth rate,
development, and survival.

Objective: To determine the effects of competition intensity in terms
of plant density and composition on plant survival and growth relative
to soil moisture availability. Also, this study will be designed to
determine at what levels of competition moisture becomes limiting to
survival, and what species have superior competitive abilities.

Justification: Under natural conditions the presence of native undesirable
plants may retard or prevent the successful establishment of artificially
revegetated species through intensive competition for environmental
factors. The principle factor most limiting is moisture, and when
competition is severe, moisture is usually the single factor for which
the greatest demand is made. Competition may be interspecific, as among
many different species, or it may be intraspecific, as among individuals
of the same species. Intraspecific competition is usually the most
severe, and its effects are particularly critical to revegetation in
terms of seeding and planting rates. The control of interspecific
competition is also vitally important.

Study Methods: Plants will be grown under controlled conditions in
phytometers. Intraspecific competition studies will be conducted for
various ages and stages of development of each species, under various
density conditions. Interspecific competition studies will involve, at
various stages of development of each species, different densities of
species combinations grown together. Competition effects will be studied
in terms of plant vigor, yield, ground area covered, and survival of each
species. Also, special morphological developments, such as total root
growth and rate, will be determined for each treatment effect. The amount
and rate of moisture depletion will be determined for each treatment,
and the levels at which moisture becomes limiting to survival will be
determined. The effects of increasing competition intensity on the
internal water balance under various soil water regimes will be determined.

Time Requirement: Three years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

Priority B3

Study Title: The nutrient requirements of plants and the effects of elemental competition and environmental factor interactions on the survival and growth of selected species.

Objective: To determine for each selected species, at various stages of growth, what nutritional levels and elemental constituents are most limiting to growth and survival, and to determine the effects of elemental competition and environmental factor interactions on plant growth and survival.

Justification: The many studies concerning plant responses to fertilization under natural conditions indicate that mountain soils on exposed sites are usually most deficient in N, P, and K. There is also considerable evidence which indicates that various important micronutrients may also be deficient. For the most part, the nutrient requirements for the various stages of growth for species commonly used in artificial revegetation have not been determined. There is also considerable evidence indicating the importance of elemental competition, wherein the presence of certain nutrients prohibit use by the plant of various essential elements. Also, the effects of environmental factors, such as moisture and temperature conditions, have not been adequately determined for the various species used in revegetation.

Study Methods: For each species at various stages of development, and under controlled environmental conditions, various nutrient combination levels in the sand culture media will be studied relative to growth and development, vigor, production, and survival. Also, elemental competition will be studied under nutrient conditions representative of harsh sites, by supplying given quantities of elements known to be antagonistic to the availability of other elements (for instance, P for Zn). Under controlled nutrient conditions, variations in environmental conditions will be studied relative to their effect on various combinations of nutrient availability in terms of growth and development.

Time Requirement: Three years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

Priority B4

Study Title: The influence of inter- and intraspecific competition intensity on radiation intensity, quality, and duration, and its effects on the survival and growth of selected species.

Objective: To determine to what degree radiation is affected by various intensities of plant competition, and the effects of these radiation variations on plant growth and development.

Justification: Under an overstory of undesirable species, revegetation species may be subjected to considerably different light conditions than those encountered in open areas, and those required for growth and survival. For maximum growth and development, each species has an optimum light requirement, which when deficient to some critical level, even though other environmental factors are satisfactory, may prevent survival and optimum growth. Light is seldom a direct limiting factor except under conditions of intense competition.

Study Methods: Plants of each species, at various stages of growth, will be subjected to various intensities of competition by overstory species and degrees of shading. Under controlled conditions of moisture and temperature, the effects of variations in radiation intensity, quality, and duration will be determined in terms of plant growth rate, morphological development, and survival. The degree of sophistication in instrumentation is yet to be determined because of the rapid changes and advances being made in this field. There is some possibility that field studies may be conducted in conjunction with laboratory investigations.

Time Requirement: Two years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

Priority C1

Study Title: Methods of breaking bud and seed dormancy, and the effects of environmental stress on germination and bud growth for plant species selected for revegetation.

Objectives: To determine methods of breaking seed and bud dormancy and promoting germination in seeds of species that require special treatment for germination at optimum periods of environmental conditions. To determine at what levels of environmental stress various factors become limiting to seed germination and bud development.

Justification: There are numerous seeding trials reported in the literature indicating that seed has failed to germinate during the first season, and during periods of optimum conditions for growth. This results in seed loss due to rodent activity, and bud damage by insects and fungal attacks. Also, under extreme stress conditions seeds may not germinate, or buds may not develop, thus contributing to loss of stand development.

Study Methods: Method and techniques will be studied and evaluated for breaking seed and bud dormancy of species selected for harsh site revegetation. These treatments will include various levels of chemical and physical scarification, stratification treatments, and applications of hormones and combinations of light treatments. Osmotic solutions at various concentrations will be used to evaluate the effects of water stress on seed germination, and soil water stress will be evaluated in terms of bud development and growth. Germination and bud growth relative to stress effects of temperature, radiation, and light will also be studied. These studies will, for the most part, be restricted to the laboratory, but some field trials will also be made.

Time Requirement: Two years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

Priority C2

Study Title: The effects of growth regulators on the survival and growth of plant species selected for revegetation.

Objective: To determine what growth regulators, in what concentrations, and in what quantities, will promote plant growth rates following germination, and to what degree growth promotion will facilitate seedling survival, root development, maturation growth and development, and plant survival.

Justification: Following germination, many seedlings are unable to survive and maintain a sufficient growth rate due to limiting environmental conditions. One of the primary causes of seedling mortality is soil moisture depletion in the zone most critical to the seedling, in the upper few inches of soil. During periods of rapid soil drying, it may be possible to promote or increase growth rates, particularly of seedling radicles, in order to penetrate to depths of sufficient moisture availability, and to maintain a root growth rate which exceeds the rate of surface drying.

Study Methods: There are many plant growth regulators—hormones—that can be applied to plant media in nutrient solutions, some of which are pyridoxine, thiamine, and nicotinic acid needed for root growth, adenine for leaf growth, and hormones of the auxin group for stem growth. Various concentrations of these hormonal substances, and others, will be applied through nutrient solution to plants to determine their effect on subsequent growth rates. Also, they will be used to determine their effects on inhibition of growth through periods of environmental stress.

Time Requirement: Two years.

Location: Forestry Sciences Laboratory, Logan, Utah.

Personnel: One professional and one technician.

PERSONNEL AND FACILITIES REQUIRED

Personnel Required

The existing personnel status at Logan is inadequate to carry out all the studies proposed. Table 1 summarizes, by study priority, duration in years, man-year requirements per calendar year, and the total man-years required to complete each study. Table 2 summarizes the study and personnel schedule in terms of man-years per calendar year by study priority. The number of available and needed personnel to carry out the desired program of research is summarized in Table 3.

Study duration in years was assigned primarily on the basis of physiological considerations. Some consideration was given to time for the development of study techniques, growth of plants, and selection of species to be studied. Also, in some instances the total number of man-years spent on a study may be less than the number of years of the study duration. For instance, study A2 will require a total duration of two years (Table 1) to be completed, yet only one man-year will be required (Table 2). Better use of greenhouse and growth chamber facilities can be made in such studies where either similar procedures, or similar plant growth stages are being studied if done at the same time.

Table 1. Personnel requirements for desired program of research.

Study Priority	Duration Years	Man-Years Per Calendar Year	Time Required Man-Year		Man-Years
			Prof.	Non-Prof.	
A1	4	1	1/2	1/2	4
A2	2	1/2	1/4	1/4	1
B1	2	1/2	1/4	1/4	1
B2	3	1	1/2	1/2	3
B3	3	1	1/2	1/2	3
B4	2	1	1/2	1/2	2
C1	2	1 1/2	1	1/2	3
C2	2	1 1/2	1	1/2	3

Table 2. Study and personnel schedule in man-years (including professional and non-professional personnel.

Study Priority	Years of Proposed Research Program												Total Study Man-Years
	1		2		3		4		5		6		
	P[1]	N-P[2]	P	N-P	P	N-P	P	N-P	P	N-P	P	N-P	
A1	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2					4
A2			1/4	1/4	1/4	1/4							1
B1					1/4	1/4	1/4	1/4					1
B2					1/2	1/2	1/2	1/2	1/2	1/2			3
B3							1/2	1/2	1/2	1/2	1/2	1/2	3
B4									1/2	1/2	1/2	1/2	2
C1									1	1/2	1	1/2	3
C2									1	1/2	1	1/2	3
Man-Years	1/2	1/2	3/4	3/4	1 1/2	1 1/2	1 3/4	1 3/4	3 1/2	2 1/2	3	2	20

1/ Professional personnel

2/ Non-professional personnel

Table 3. Available and needed personnel for desired program of research.

Man-Power Schedule	Year of Research Program					
	1	2	3	4	5	6
Man-Years Required	1	1½	3	3½	6	5
Man-Years Available						
Research Forester—Brown	½	¼	½	¼	½	½
Research Forester—Richardson			¼			
Physiologist—McDonough (1704)		¼	¼	¼	¼	¼
Technician—Voeller	¼	½	¼	½	½	¼
Total Man-Years Available	1	1¼	1½	1¼	1¼	1¼
Deficit (Man-Years)	0	¼	1½	2¼	4 3/4	3 3/4
Man-Years Required						
Project Scientists			1	1	2 3/4	2½
Technicians		½	½	1¼	2	1½

Under present personnel conditions at Logan, studies A1, A2, and B1 can possibly be conducted and completed. One of the objectives of these studies is to provide a basis for extending basic research results to field trials and practical applications. Therefore, approximately one-half of each calendar year will be spent on field studies of physiological requirements and revegetation techniques. Because of the nature of the physiological studies described above, time allowances will be readily flexible to conditions dictated by local climatic conditions. For instance, when weather or season will not permit field study, laboratory studies may be continued throughout the winter months. It may even be possible to conduct laboratory studies concurrently with field studies during the field season. For this reason, as shown in Table 3, for Brown and Voeller only one-half man-year is accounted for during each calendar year.

It has been agreed that personnel from Projects 1603 and 1704 will cooperate on certain studies that cover material of mutual interest and need. In this sense, it may be that the priorities of certain studies may, by necessity through opportunity, change as the result of personnel and facilities availability. Some of the work that McDonough is currently planning for the near future has been scheduled in this problem analysis for a much later date, as for instance, studies C1 and C2. It may be that through an extension of these studies by Project 1704 to include those species of interest to Project 1603, a certain amount of delay as shown in the schedule (Table 2) will be overcome. The study and personnel schedules as presented above are representative of study priorities, but

a great deal of flexibility has also been written into them for the purpose of cooperative research and occurrence of opportunity.

As scheduled, the proposed research program will require that Project 1603 acquire at least three additional project scientists and two full time technicians. This will need to be accomplished some time between the fourth and fifth year of this program to reduce the work load and permit an expansion of field studies conducted on revegetation techniques.

Facilities Required

At the present time there is inadequate laboratory and office space, and inadequate equipment to carry out this research program.

Facilities Available

1. One physiology laboratory and soil physics laboratory

2. Two offices

3. Greenhouse facilities

Facilities Needed

1. Office space

2. Additional glasshouses (a minimum of two)

3. Growth chamber facilities

4. Expansion of headhouse facilities to include more working area and equipment.

LITERATURE CITED

Aderikhin, P. G. 1954. The effect of the colour of soil on its temperature and fertility. Trudy voronezh Univ. 26:56-92. (Russian, Eng. Summary).

Amen, R. D. 1963. The concept of seed dormancy. Amer. Sci. 51:408-424.

Anderson, H. W. 1947. Soil freezing and thawing as related to some vegetation, climatic and soil variables. Jour. For. 45:94-101.

Arakeri, H. R. and A. R. Schmid. 1949. Cold resistance of various legumes and grasses in early stages of growth. Agron. J. 41:182-185.

Ashby, W. C. and H. Hellmers. 1955. Temperature requirements for germination in relation to wild-land seeding. J. Range Mgt. 8:80-83.

Bailey, L. F. 1940. Some water relations of three western grasses. II. Drought resistance. III Root development. Amer. J. Bot. 27:129-135.

Bailey, R. W., C. W. Craddock, and A. R. Croft. 1947. Watershed management for summer flood control in Utah. USDA Misc. Publ. No. 639. 24 pp.

Baum, W. A. 1949. On the relation between mean temperature and height in the layer of air near the ground. Ecology 30:104-107.

Billings, W. D. 1957. Physiological ecology. Ann. Rev. Plant Physiol. 8:375-392.

Blaisdell, J. P. 1949. Competition between sagebrush seedlings and reseeded grasses. Ecology 30:512-519.

Bleak, A. T. 1959. Germination characteristics of grass seed under snow. J. Range Mgt. 12:298-302.

Bleak, A. T. 1963. Annual progress report: range revegetation investigations. Crops Res. Div., ARS, USDA 100 pp.

Bliss, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. Arctic 15:117-144.

Bonner, J. and A. W. Galston. 1958. Principles of Plant Physiology. W. H. Freeman. San Francisco. 499 pp.

Branson, F. A. 1953. Two new factors affecting resistance of grasses to grazing. J. Range Mgt. 6:165-171.

Britten, E. J. 1961. The influence of genotype and temperature on
flowering in Trifolium repens. Agron. J. 53:11-14.

Brown, J. C. 1963. Interactions involving nutrient elements. Ann.
Rev. Plant Physiol. 14:93-106

Buckman, H. O. and N. C. Brady 1960. The nature and properties of
soils. Macmillan. New York. 567 pp.

Carroll, J. C. 1943. Atmospheric drought tests of some pasture and
turf grasses. J. Amer. Soc. Agron. 35:77-79.

Cassady, J. T., and G. E. Glendening. 1940. Revegetating semidesert
range lands in the southwest. U. S. Forest Service. Southwestern
Forest and Range Expt. Sta. Forestry Publ. No. 8. 22 pp.

Cathey, H. M. 1964. Physiology of growth retarding chemicals. Ann.
Rev. Plant Physiol. 15:271-302.

Cook, C. W. 1965. Plant and livestock responses to fertilized rangelands
Utah Agr. Expt. Sta. Bul. 455. 35 pp.

Cook, C. W., P. D. Leonard, and C. D. Bonham. 1965. Rabbitbrush competi-
tion and control on Utah rangelands. Utah Agr. Expt. Sta. Bul. 454.
28 pp.

Cook, C. W. and C. E. Lewis. 1963. Competition between big sagebrush and
seeded grasses on foothill ranges in Utah. J. Range Mgt. 16:245-250.

Craddock, G. W. and C. L. Forsling. 1938. The influence of climate and
grazing on spring-fall sheep range in southern Idaho. USDA Tech.
Bul. No. 600. 42 pp.

Cumming, B. G., S. B. Hendricks, and H. A. Borthwick. 1965. Rhythmic
flowering responses and phytochrome changes in a selection of Chenopodium
rubrum. Canadian J. Bot. 43:825-853.

Daubenmire, R. 1943. Soil temperature versus drought as a factor deter-
mining lower altitudinal limits of trees in the Rocky Mountains. Bot.
Gaz. 105:1-13.

Daubenmire, R. 1957(a). Influence of temperature upon moisture constants
and its possible ecologic significance. Ecology 38:320-324.

Daubenmire, R. 1957(b). Injury to plants from rapidly dropping temper-
atures in Washington and northern Idaho. J. For. 55:581-585.

Daubenmire, R. 1959. Plants and Environment. John Wiley. New York.
422 pp.

Decker, A. M. T. S. Ronningen. 1957. Heaving in forage stands and in bare ground. Agron. J. 49:412-415.

Dewey, D. R. 1962. Breeding crested wheatgrass for salt tolerance. Crop Sci. 2:403-407.

Eck, H. V., V. L. Hauser, and R. H. Ford. 1965. Fertilizer needs for restoring productivity on Pullman silty clay loam after various degrees of soil removal. Soil Sci. Soc. Amer. Proc. 29:209-213.

Eckert, R. E. and A. T. Bleak. 1960. The nutrient status of four mountain rangeland soils in western Nevada and eastern California. J. Range Mgt. 13:184-188.

Eckert, R. E., A. T. Bleak, and J. H. Robertson. 1961. Effects of macro- and micronutrients on the yield of crested wheatgrass. J. Range Mgt. 14:149-155.

Eckert, R. E. and R. A. Evans. 1963. Responses of downy brome and crested wheatgrass to nitrogen and phosphorus in nutrient solution. Weeds 11:170-174.

Eckert, R. E. and R. A. Evans. 1965. Mountain meadow restoration. Res. Range Mgt. Univ. Nevada R13:37.

Ellison, L. 1949. Establishment of vegetation on depleted subalpine range as influenced by microenvironment. Ecol. Monog. 19:95-121.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecol. Monog. 24:89-184.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26:1-78.

Everson, A. C. 1951. Grass yields of three differently treated range areas. J. Range Mgt. 4:93-94.

Fehl, A. J. and W. Lange. 1965. Soil stabilization induced by growth of microorganisms on high-calorie mold nutrients. Soil Sci. 100-368-374.

Forsling, C. L. and W. A. Dayton. 1931. Artificial reseeding on western mountain range lands. USDA Circ. No. 178. 44 pp.

Frischknecht, N. C. 1951. Seedling emergence and survival of range grasses in central Utah. Agron. J. 43:177-182.

Frischknecht, N. C. 1963. Contrasting affects of big sagebrush and rubber rabbitbrush on production of crested wheatgrass. J. Range Mgt. 16:70-74.

Gardner, F. P. and W. E. Loomis. 1953. Floral induction and development in orchard grass. Plant Physiol. 28:201-217.

Gates, D. H., L. A. Stoddart, and C. W. Cook. 1956. Soil as a factor influencing plant distribution on salt deserts of Utah. Ecol. Monog. 26:155-175.

Gates, D. M. 1962. Energy Exchange in the Biosphere. Harper and Row. New York. 151 pp.

Gates, D. M. and C. M. Benedict. 1963. Convection phenomena from plants in still air. Amer. J. Bot. 50:563-573.

Gauch, H. G. 1957. Mineral nutrition of plants. Ann. Rev. Plant Physiol. 8:31-64.

Gerloff, G. C. 1963. Comparative mineral nutrition of plants. Ann. Rev. Plant Physiol. 14:107-124.

Gessel, S. P. 1962. Progress and problems in mineral nutrition of forest trees. In: Koslowskii, T. T. Tree Growth. Ronald Press. New York. pp. 221-235.

Grime, J. P. 1965. Shade tolerance in flowering plants. Nature 208:161-163.

Gritton, E. T. and R. E. Atkins. 1963. Germination of grain sorghum as affected by freezing temperatures. Agron. J. 55:139-142.

Harlan, J. R. 1951. New grasses for old ranges. J. Range Mgt. 4:16-18.

Haupt, H. F. 1956. Nitrogen loss from granitic soils on cheatgrass brome range. For. Sci. 2:268-272.

Hedrick, D. W., D. N. Hyder, and F. A. Sneva. 1964. Overstory-understory grass seedings on sagebrush bunchgrass range. Oregon Agr. Expt. Sta. Tech. Bul. 80. 31 pp.

Hellmers, H. 1963. Some temperature and light effects in the growth of Jeffrey pine seedlings. For. Sci. 9:189-201.

Hermann, R. K. 1963. Temperature beneath various seedbeds on a clearcut forest area in the Oregon Coast Range. Northwest Sci. 37:93-103.

Hopkins, H. 1953. Root development of grasses on revegetated land. J. Range Mgt. 6:382-392.

Hull, A. C. 1960. Winter germination of intermediate wheatgrass on mountain lands. J. Range Mgt. 13:257-260.

Hull, A. C. 1963. Competition and water requirements of cheatgrass and wheatgrasses in the greenhouse. J. Range Mgt. 16:199-204.

Hull, A. C. and R. C. Holmgren. 1964. Seeding southern Idaho rangelands. U. S. Forest Service. Res. Paper INT-10. 32 pp.

Humphrey, R. R. 1962. Range Ecology. Ronald Press. New York. 234 pp.

Hunter, J. R. and E. E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron. J. 44:107-109.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8:257-274.

Jameson, D. A. 1961. Heat and desiccation resistance of tissue of important trees and grasses of the pinyon-juniper type. Bot. Gaz. 122-174-179.

Jameson, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.

Jones, M. B., C. M. McKell, and S. S. Winans. 1963. Effect of soil temperature and nitrogen fertilization on the growth of soft chess (Bromus mollis) at two elevations. Agron. J. 55:44-46.

Julander, O. 1945. Drought resistance in range and pasture grasses. Plant Physiol. 20:573-599.

Keneflck, D. G. 1964. Cold acclimation as it relates to winter hardiness in plants. Agr. Sci. Rev. 2(4):21-31.

Kenesarina, N. 1959. Special characteristics of the water regime and drought resistance of tree and shrub species in central Kazakhstan. Sel' shoe Khozgaistvo Kazakhstana 10:82-85.

Kershaw, K. W. 1964. Quantitative and Dynamic Ecology. American Elsevier. New York. 183 pp.

Klikoff, L. G. 1965(a). Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. Ecol. Monog. 35:187-211.

Klikoff, L. G. 1965(b). Photosynthetic response to temperature and moisture stress of three timberline meadow species. Ecology 46:516-517.

Knipe, D. and C. H. Herbel. 1960. The effects of limited moisture on germination and initial growth of six grass species. J. Range Mgt. 13:297-302.

Koshi, P. T. and G. K. Stephenson. 1962. Shade and mulch as influences
on loblolly pine seedlings and their immediate environment. For. Sci.
8:191-204.

Kozlowski, T. T. 1957. Effect of continuous high light intensity on
photosynthesis of forest tree seedlings. For. Sci. 3:220-224.

Kozlowski, T. T. 1964. Water metabolism in plants. Harper and Row.
New York. 227 pp.

Kramer, P. J. 1957. Some effects of various combinations of day and
night temperatures and photoperiod on the height growth of loblolly
pine seedlings. For. Sci. 3:45-55.

Kramer, P. J. 1962. The role of water in tree growth. In: Kozlowski,
T. T. Tree Growth. Ronald Press. New York. pp. 171-182.

Kramer, P. J. 1963. Water stress and plant growth. Agron. J. 55:31-35.

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of trees. McGraw
Hill. New York. 642 pp.

Lang, A. 1952. Physiology of flowering. Ann. Rev. Plant Physiol. 3:265-306.

Langridge, J. 1963. Biochemical aspects of temperature response. Ann.
Rev. Plant Physiol. 14:441-462.

Larson, P. R. 1965. Stem form of young Larix as influenced by wind and
pruning. For. Sci. 11:412-424.

Laude, H. M. 1956. The seedling emergence of grasses as affected by low
temperature. Agron. J. 48:558-560.

Laude, H. M. and B. A. Chaugule. 1953. Effect of stage of seedling
development upon heat tolerance in bromegrasses. J. Range Mgt. 6:320-324.

Laude, H. M., J. E. Shrum, and W. E. Biehler. 1952. The effect of high
soil temperatures on the seedling emergence of perennial grasses.
Agron. J. 44:110-112.

Lavin, F. and H. W. Springfield. 1955. Seeding in the southwestern pine
zone for forage improvement and soil protection. USDA Agr. Handbook
No. 89. 52 pp.

Leopold, A. C. 1964. Plant Growth and Development. McGraw Hill. New
York. 466 pp.

McKell, C. M., J. P. Robinson, and J. Major. 1962. Ecotypic variation in
medusahead, and introduced annual grass. Ecology 43:686-698.

McGinnies, W. J. 1960. Effect of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

Maguire, W. P. 1955. Radiation, surface temperature, and seedling survival. For. Sci. 1:277-284.

Marston, R. B. 1956. Air movement under aspen forest and on an adjacent opening. J. For. 54:468-469.

Maynard, M. L. and D. H. Gates. 1963. Effects of wetting and drying on germination of crested wheatgrass seed. J. Range Mgt. 16:119-121.

Mergen, F. 1963. Ecotypic variation in Pinus strobus L. Ecology 44:716-727.

Miller, D. E. and W. C. Bunger. 1963. Use of plastic soil covers in sweet corn production. Agron. J. 55:417-419.

Mooney, H. A., R. D. Hillier, and W. D. Billings. 1965. Transpiration rates of alpine plants in the Sierra Nevada of California. Amer. Midland Nat. 74:374-386.

Morris, M. S. 1960. Range management: a statement of its aims, principles, techniques and problems. Montana Forest and Conserv. Expt. Sta. Bul. No. 13. 14 pp.

Mueggler, W. F. and J. P. Blaisdell. 1951. Replacing wyethia with desirable forage species. J. Range Mgt. 4:143-150.

Nelson, E. W. 1934. The influence of precipitation and grazing upon black grama grass range. USDA Tech. Bul. No. 409. 32 pp.

Nord, E. C. 1965. Autecology of bitterbrush in California. Ecol. Monog. 35:307-334.

Olmsted, C. E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve strains of side-oats grama. Bot. Gaz. 106:46-74.

Oosting, H. J. 1956. The study of plant communities. W. H. Freeman. San Francisco. 440 pp.

Packer, P. E. 1953. Effects on trampling disturbance on watershed condition, runoff, and erosion. J. For. 51:23-31.

Packer, P. E. 1964. Problem analysis for the protection, restoration, and management of range watersheds to reduce flood runoff, control erosion, and prevent sedimentation. U. S. Forest Service. INT. 65 pp. (Unpubl.)

Pallas, J. E., D. G. Harris, C. B. Elkins, and A. R. Bertrand. 1963. Research in plant transpiration. USDA Agr. Res. Serv. Prod. Res. Report No. 70. 37 pp.

Passey, H. B. and V. K. Hugie. 1963. Variation in bluebunch wheatgrass in relation to environment and geographic location. Ecology 44:158-161.

Peacock, J. T. and C. McMillan. 1965. Ecotypic differentiation in Prosopis (Mesquite). Ecology 46:35-51.

Pellett, H. M. and E. C. Rogerts. 1963. Effects of mineral nutrition on high temperature induced growth retardation of Kentucky bluegrass. Agron. J. 55:473-476.

Peterson, H. B. and R. L. Smith. 1964. Minor element recommendations for Utah crops. Utah Agr. Expt. Sta. Circ. 146. 11 pp.

Peterson, M. L. and W. E. Loomis. 1949. Effects of photoperiod and temperature on growth and flowering of Kentucky bluegrass. Plant Physiol. 24:31-43.

Plummer, A. P., A. C. Hull, G. Stewart, and J. H. Robertson. 1955. Seeding rangelands in Utah, Nevada, southern Idaho, and western Wyoming. USDA Agr. Handbook, No. 71. 73 pp.

Potter, L. D. 1953. Seedling growth and soil drought resistance of Northern Great Plains legumes, alfalfa, and four grasses. J. Range Mgt. 6:399-404.

Power, J. F., D. L. Grunes, W. O. Willis, and G. A. Reichman. 1963. Soil temperature and phosphorus effects upon barley growth. Agron. J. 55:389-392.

Reifsnyder, W. E. and H. W. Lull. 1965. Radiant energy in relation to forests. U. S. Dept. Agr. Forest Serv. Tech. Bul. No. 1344. 111 pp.

Robertson, J. H. and C. K. Pearse. 1945. Artificial reseeding and the closed community. Northwest Sci. 19:58-66.

Rogler, G. A. 1943. Response of geographical strains of grasses to low temperature. J. Amer. Soc. Agron. 35:547-559.

Rosenquist, D. W. and D. H. Gates. 1961. Responses of four grasses at different stages of growth to various temperature regimes. J. Range Mgt. 14:198-202.

Ruf, R. H. 1966. Native Sierra Nevada plant shows problem solving potential. Nevada Ranch and Home Rev. 3(4):8-11.

Ruf, R. H. and E. Farmer. 1964. Study plan for establishment of _Ceanothus prostratus_ on sites similar to, but geographically distant from its native habitat. U. S. Forest Service. INT (unpubl.) 9 pp.

Sampson, A. W. 1959. Range Management: Principles and practices. John Wiley. New York. 570 pp.

Satoo, T. 1962. Wind, transpiration, and tree growth. In: Kozlowski, T. T. (ed.). Tree Growth. Ronald Press. New York. 299-310.

Schultz, A. M. and H. H. Biswell. 1952. Competition between grasses reseeded on burned brushlands in California. J. Range Mgt. 5:338-345.

Scott, V. H. and R. H. Burgy. 1956. Effects of heat and brush burning on the physical properties of certain upland soils that influence infiltration. Soil Sci. 82:63-70.

Shields, L. M. and L. W. Durrell. 1964. Algae in relation to soil fertility. Bot. Rev. 30:92-128.

Siegelman, H. W. and W. L. Butler. 1965. Properties of phytochrome. Ann. Rev. Plant Physiol. 16:383-392.

Singh, R. and R. B. Alderfer. 1966. Effects of soil moisture stress at different periods of growth of some vegetable crops. Soil Sci. 101:69-80.

Slatyer, R. O. 1957. The significance of the permanent wilting percentage in studies of plant and soil water relations. Bot. Rev. 23:585-636.

Slatyer, R. O. 1960. Absorption of water by plants. Bot. Rev. 26:331-392.

Smith, R. S., R. F. Scharpf, and E. R. Schneegas. 1965. Frost injury to bitterbrush in eastern California. U.S. Forest Serv. Res. Note PSW-82. 4 pp.

Stewart, G. and A. C. Hull. 1949. Cheatgrass (_Bromus tectorum_) — an ecologic intruder in southern Idaho. Ecology 30:58-74.

Stoddart, L. A. 1946. Seeding arid ranges to grass with special reference to precipitation. Utah Agr. Expt. Sta. Circ. 122. 29 pp.

Stoddart, L. A. and A. D. Smith. 1955. Range Management. McGraw Hill. New York. 433 pp.

Stone, E. L. and G. M. Will. 1965. Boron deficiency in _Pinus radiata_ and _P. pinaster_. Forest Sci. 11:425-433.

Storey, H. C. 1960. Watershed research needs and probable future trends in watershed management. J. For. 58:312-316.

Tabler, R. D. 1964. The root system of Artemisia tridentata at 9,500 feet in Wyoming. Ecology. 45:633-636.

Tew, R. K., S. A. Taylor, and G. L. Ashcroft. 1963. Influence of soil temperature on transpiration under various environmental conditions. Agron. J. 55:558-560.

Thames, J. L. 1961. Effects of wax coatings on leaf temperature and field survival of Pinus taeda seedlings. Plant Physiol. 36:180-182.

Timm, H., L. J. Clemente, J. W. Perdue, K. G. Bayhott, and B. J. Hoyle. 1966. Micronutrient deficiencies of copic bay soils in Tulelake Basin. Calif. Agr. 20(2):6-7.

Tisdale, E. W. 1962. The ecotypic concept in range management. Scottish Plant Breeding Sta. Record. 8 pp.

U. S. Dept. Agric. 1966. Reclaiming Sunlight. Agr. Res. 14(8):7.

Ursic, S. J. 1961(a). Early survival of loblolly plantings on eroded lands. Tree Planter's Notes No. 53:27-28.

Ursic, S. J. 1961(b). Lethal root temperatures of 1-0 loblolly pine seedlings. Tree Planter's Notes No. 47:25-28.

Wallace, A. 1965. Micronutrient deficiencies in plants and their correction with chelates. Agr. Sci. Rev. 3(1):18-24.

Weihing, R. M. 1963. Growth of ryegrass as influenced by temperature and solar radiation. Agron. J. 55:519-521.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Sci. 147:250-260.

Wraight, M. J. 1965. Growth rates and potential for spread of alpine carpet grass, Chionochloa (Danthonia) australis. New Z. J. Bot. 3:171-179.

Younis, M. A., F. C. Stickler, and E. L. Sorensen. 1963. Reactions of seven alfalfa varieties under simulated moisture stresses in the seedling stage. Agron. J. 55:177-182.

Zelitch, I. (ed.) 1963. Stomata and water relations in plants. Conn. Agr. Expt. Sta. Bul. 664. 116 pp.